The role of body size in predator-prey interactions and community structure

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For my family

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Abstract

Body size is a fundamental property of an organism. Consistent body size-related patterns, relevant to food webs, have been found at the individual (e.g. metabolism), population (e.g. predator-prey interactions), and community (e.g. body-size scaling with abundance) levels of ecological organisation. These patterns represent key components of food webs, so body-size distributions should be representative of a wide range of food web processes. Therefore, knowledge on the controls of the distribution of body sizes within a community should aid in the understanding of community structure and stability. I focused on two key body size-associated relationships in food webs: the relationship between body mass/size (M) and abundance (N), and relationships between body size and predator-prey interaction strengths.

Analysis of M-N data, collected from stream communities spanning habitat size and flooding disturbance gradients, indicated that habitat size limited top predator size, whereas disturbance limited their abundance. These results highlight how M-N relationships, and changes in body size patterns across communities in general, are particularly useful tools for understanding influences on community structure.

Mesocosm experiments were used to investigate how relationships between predator-prey body mass ratios (PPMR) and predator-prey interaction strengths differed when prey defences and density varied. Larger predators generally had stronger per-capita interaction strengths however, prey morphological defences and prey abundance significantly altered the relationship between body size and per-capita interaction strengths. Defended prey were eaten less than undefended prey and the relationship between PPMR and interaction strength was steeper at higher prey densities. These results indicated that while PPMRs are generally

good predictors of interaction strengths, the incorporation of other general traits, beyond body size, into current theory would improve prediction of interaction strengths in food webs.

An in-stream channel experiment was conducted to investigate the population, compared to per-capita, effects of top-predator body size and abundance on the strength of top-down interactions in food webs. By manipulating top-predator size and abundance, but keeping top-predator (brown trout) biomass constant, I showed that smaller, more abundant top predators had greater top-down effects compared to, fewer large predators of equivalent biomass.

Overall, my results indicate that body size-related relationships can be used to describe changes in predator-prey interaction strengths, community structure and by extension possibly community stability. However, the usefulness of these relationships could be improved by incorporating traits over and above body size, which would aid in the prediction of community stability as communities face ongoing anthropogenic pressures.

Chapter One

Introduction

Ecological communities are under extreme pressure from increased anthropogenic stressors (Vitousek et al. 1997, Sala et al. 2000). Consequently, understanding mechanisms which drive changes in community stability (i.e. ability to be resistant and resilient to perturbations) are important for the conservation of biodiversity (McCann 2000, Montoya et al. 2006). Ecological communities are difficult to study because they are naturally complex, often with many species, multiple trophic levels, and a myriad of different interactions which connect individuals (e.g. Polis 1991). Moreover, emergent community patterns are inherently a result of interplay between both physical environmental abiotic factors and biotic interactions between organisms (Power et al. 1988, Wellborn et al. 1996). Consequently, although essential for the future conservation of ecological communities, determining which processes control community structure and stability is particularly challenging.

Food webs are important descriptors of ecological communities and are a common tool used to measure and understand community structure and stability (Thompson et al. 2012). Food webs describe the connections between predators and prey, predominantly via feeding interactions (Cohen et al. 1993, Dunne 2009). Information on both the connections between species and also the strength of those connections is important for predicting and understanding food web stability (McCann 2000, Dunne et al. 2002, Montoya et al. 2006). Because food web stability and ecological function are dependent on the network of interactions between individuals or species in a community (Tylianakis et al. 2007, Thompson et al. 2012, Schmitz et al. 2015), there has been a recent call for more network, or food web information, to be used in biomonitoring and ecological management (Gray et al.

2014, Fraser et al. 2015). However, because communities are inherently complex, constructing detailed networks is very time- and labour-intensive, and impractical for most communities (Hegland et al. 2010, Thompson et al. 2012, Gray et al. 2014). Therefore, finding simplifying patterns or proxy variables which can readily be used to accurately infer food web interactions and structures is important for both basic and applied food-web ecology.

Recently emerging, consistent and predictable patterns related to body size in ecological networks, particularly food webs, suggests that body size might be a particularly informative proxy variable (Woodward et al. 2005). Body size is related to many fundamental properties of organisms, such as metabolism, growth rate, home range, and productivity (see Woodward et al. 2005 for review). This strong link between body size and organism-level biology means patterns related to body size may scale to higher levels of organisation from populations to entire communities (Cohen et al. 2003, Woodward et al. 2005). For example, body size is related to gape size, which is a key determinant of the size class of prey that a predator can consume (Figure 1). Therefore, in habitats where consumers often engulf their prey, as in aquatic systems, body size can be an important driver of trophic structure (Jennings et al. 2001, Petchey et al. 2008, Arim et al. 2010, Riede et al. 2011). Moreover, body size is related to metabolism, which largely underpins an organism's energetic demands (Peters 1983). This relationship between body size and metabolism has been used to explain why many patterns, such as feeding rates, seen in nature have ¼ power scaling relationships with body size (Brown et al. 2004). Therefore, changes in the distributions of body sizes within communities should provide mechanistic insights into the drivers of community structure and stability.

In this thesis I focus on two key body size-associated relationships. Firstly, the relationship between body mass/size (M) and abundance (N), and secondly relationships between body

size and predator-prey interaction strengths. Both of these relationships provide potentially important information about community structure and dynamics.

Body mass-abundance relationships

The relationship between M and N is one of the most well documented allometric scaling relationships (White et al. 2007). In general, there is a negative linear relationship between M and N when using logarithmically transformed data, and the slope of this relationship is commonly considered to be - 0.75 within a trophic level and - 1.0 across trophic levels. For these M-N relationships to exist, communities must have many small individuals and relatively fewer large individuals (Figure 1). Because an individual's body size is related to aspects of community structure, such as its trophic position and abundance (Jennings et al. 2001, Cohen et al. 2003, Arim et al. 2010, Riede et al. 2011), and because M-N relationships can alternately be represented as Eltonian ecological pyramids (Trebilco et al. 2013), M-N relationships link individual-level traits to the structure of whole communities (Figure 1). Therefore, M-N relationships are a potentially powerful tool for summarising and assessing community structure. Moreover, changes in environmental conditions that differentially affect different size classes should be highlighted by changes in M-N relationships (Figure 1).

Body size and predator-prey interaction strengths

Over and above determining changes in community structure, determining the relative distributions of interaction strengths within a food web is also fundamentally important for determining food web stability (de Ruiter et al. 1995, McCann et al. 1998). Both theoretical and empirical studies indicate complex communities are more likely to be stable if the distribution of interaction strengths within food webs is skewed towards many weak and only a few strong interactions (de Ruiter et al. 1995, McCann 2000, Emmerson and Raffaelli

2004). However, interaction strengths are difficult to measure empirically, requiring a series of experimental manipulations for each predator-prey pairing, and consequently it is almost impossible to empirically measure all interaction strengths in an entire natural food web (Morales-Castilla et al. 2015).

Body size potentially constrains predator-prey interactions at different stages of the predation process (e.g. attack rate, speed of predator and prey movement, handling time, and digestion rates), and is also related to metabolism (Peters 1983, Woodward and Warren 2007). Therefore, body size should be related to interaction strengths in food webs (Emmerson and Raffaelli 2004, Brose et al. 2008, Schmitz and Price 2011). For example, empirical and theoretical evidence suggests that predator-prey body mass ratios (PPMRs) should be good predictors of interaction strengths in food webs (Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004). Although body size and PPMRs appear to be useful predictors of food web interaction strengths, species-specific traits such as predator foraging mode and prey vulnerability potentially modify the relationship between body size and interaction strength (e.g. Klecka and Boukal 2013). Therefore, to better estimate interaction strengths in food webs, more empirical studies are required to test whether general traits of predators and prey, independent of body size, affect interaction strengths.

Thesis structure and chapter outlines

This thesis has been written as a series of four stand-alone papers (Chapters Two to Five) which address each of the above topic areas and issues. Because these chapters will be submitted for publication, there is some repetition of material between chapters. In the final chapter (Chapter Five) I integrate and further discuss the findings from the four data chapters. Each data chapter will be a co-authored publication, however the majority of work, including

analysis and writing is my own. Relevant supplementary material is included at the end of each chapter, but references for all chapters have been collated at the end of the thesis.

In Chapter Two I investigated how M-N relationships can be used to reveal changes in community structure across gradients of both habitat size and disturbance. To do this, I further developed attributes over and above the slope of M-N relationships which can be used to provide more information on changes in community structure. Additionally, I constructed M-N relationships for 24 stream communities spanning the disturbance and habitat size gradients, and used the attributes of M-N relationships to highlight how habitat size and disturbance place different constraints on community structure.

Although PPMRs have been experimentally shown to scale with per capita interaction strengths (e.g. Emmerson and Raffaelli 2004), other empirical studies investigating how other traits of predators and prey may affect this relationship are limited. Morphological defences, such as cases, shells and spines, are common in freshwater animals and can modify predator-prey interactions by making prey less vulnerable to predators (Wootton et al. 1996, Mikolajewski and Rolff 2004, Ferry et al. 2013). Therefore, to reliably estimate interaction strengths, it is important to understand how morphological defences may affect the existing relationships between PPMR and interaction strengths.

In Chapter Three I designed an experiment to specifically test how morphologically-defended prey influenced the relationship between PPMR and per-capita interaction strength. I used flow-through stream mesocosms, predatory fish and invertebrates ranging in size, as well as a range of different prey species to run multiple rounds of pair-wise feeding interaction experiments to directly quantify predator-prey interaction strengths.

The results of Chapter Three indicated that prey abundance may also affect the relationship between PPMR and interaction strength, so in Chapter Four I further investigated how prey

abundance influenced the relationship between PPMR and interaction strength by running another mesocosm experiment using both pond and stream invertebrate prey and both fish and invertebrate predators. I manipulated the density of prey to specifically test the dependence of the relationship between PPMR and interaction strength on prey density.

Although larger predators may be associated with higher per capita interaction strengths (Emmerson and Raffaelli 2004), smaller predators may have greater population level effects (Schneider et al. 2012), because they are generally more numerous and have higher mass-specific consumption rates (Chapters Two and Three). In Chapter Five, using in-stream channels, I investigated the effect of total top predator biomass on lower trophic levels. This in-stream mesocosm experiment held top predator biomass constant while manipulating the size and abundance of brown trout in each channel to compare changes in prey and algal biomass to test the biomass-independent effects of organism size on interaction strengths.

In Chapter Six, I briefly outline the key results from individual chapters and summarise these findings in relation to existing theory. I describe how they improve current understanding of body size influences on food webs, how they might be used in management, and what body size-related aspects of food web ecology should be investigated in the future.

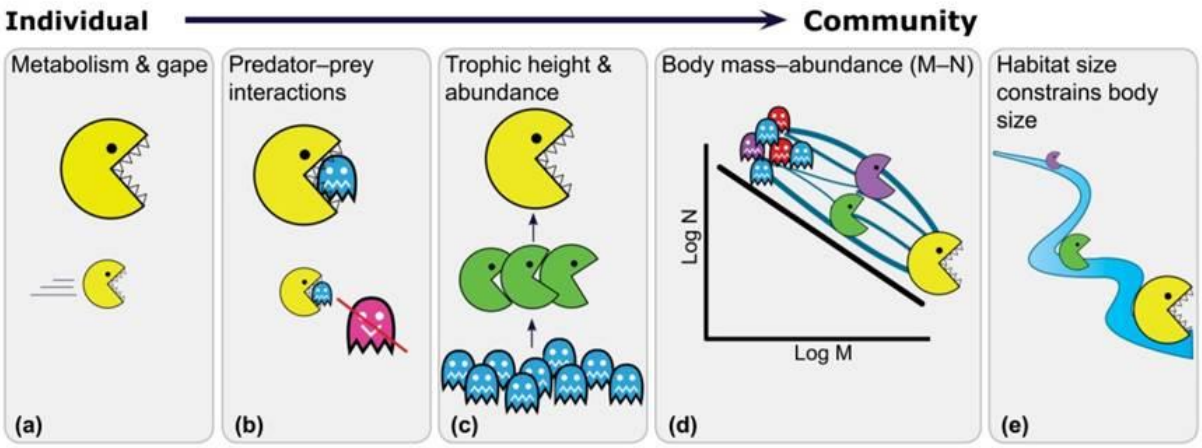


Figure 1. Cartoon diagram showing patterns related to body size from individual to community level that are particularly relevant to this thesis. Body size patterns are taxon independent, and therefore, interactions between organisms can be considered to be based solely on individual size. Hence, predators in this diagram are represented by "pacman"-like symbols which represent the body size of a generic organism. At the individual level (a), body size is related to traits such as metabolism and gape size. For example, larger organisms generally have larger gape sizes and higher total metabolic demands, but lower mass-specific metabolic rates. Therefore, body size has the potential to affect predator-prey interactions (b). For example, larger predators should be able to eat larger prey, and more prey are required to meet their higher per capita energetic demands. However, prey that are larger than predators or have traits such as morphological defences, may escape predation (b). Because body size is related to gape size, communities are often size-structured, and trophic height increases with increasing body size, and this increase in body size is often countered with a decrease in abundance (c). Consequently, it is likely that body mass-abundance (M-N) relationships (d) are a useful summary of community structure. For example, any conditions which differentially affect different size classes, such as changes in habitat size (e), which constrain top predator body size, should be reflected in changes to the M-N relationship.

Chapter Two

Body mass-abundance relationships are responsive to environmentally induced community change

Introduction

Environmental conditions influence the structure of communities by placing constraints on the abundance, size and identity of species that can live in particular habitats (Southwood 1977, Townsend and Hildrew 1994, Death 1996, Jellyman et al. 2014). Additionally, community structure depends on food-wed structure, the network of interactions between individuals and species within a community (Dunne 2009, Thompson et al. 2012). Moreover, these emergent properties are important determinants of community stability and function (Rooney and McCann 2012, Thompson et al. 2012, Schmitz et al. 2015). However, interaction networks are typically not resolved using sampling data collected for bio-monitoring or conservation purposes, probably because constructing detailed networks is very time- and labour-intensive, and therefore not currently practical across large numbers of communities (Hegland et al. 2010, Thompson et al. 2012, Gray et al. 2014). Consequently, to understand and predict how future changes in environmental conditions will drive community changes, there is a great need for proxy measures of network structure which are easier to collect and accurately capture these fundamental attributes of ecological communities.

Body mass (M)-abundance (N) relationships may providean efficient proxy of network structure and community state (Petchey and Belgrano 2010). Body mass (or body size), is related to many fundamental properties of organisms, such as metabolism, growth rate, home range, and productivity (see Woodward et al. 2005 for review). Consequently, changes to the

body size composition of communities can lead to substantial alterations at the population and community levels of ecological organisation (Woodward et al. 2005). The relationship between M and N describes how biomass is allocated among different sized organisms or species, and is generally negative across communities because smaller organisms are more abundant than larger organisms (White et al. 2007). The slope of the relationship between M and N is thought to be determined by the amount of energy available to large organisms in a community, which are in turn a function of network structure properties such as predator-prey mass ratios and trophic transfer efficiencies (Jennings 2005, Trebilco et al. 2013). Therefore, because M-N relationships link individual- and population-level traits to community structure, changes in the slope of these relationships communicate important alterations to the structure and dynamics/stability of ecosystems.

The slopes of size spectra (individual based M-N relationships, White et al. 2007) are alternative representations of traditional Eltonian ecological pyramids, and therefore explicitly link M-N patterns to community structure (Trebilco et al. 2013). Eltonian pyramids depict the number or biomass of organisms/species at different trophic levels in a community, so the shapes of these pyramids contain rich information on the structure of communities and potentially indicate the stability of particular community structures (Raffaelli 2002, Rip and McCann 2011). Steep negative M-N slopes represent "pyramid-shaped" communities with wide bases containing relatively more biomass of small organisms (i.e., lower trophic levels or prey), and fewer larger organisms at higher trophic levels (i.e., predators) which constitute a narrow pyramid apex. Conversely, shallow slopes represent communities with relatively higher biomass of large/higher-trophic-level organisms in the community compared to the biomass of lower-trophic-level organisms. Thus, because of the link between M-N relationships and Eltonian pyramids, differences in the slope of M-N relationships could be useful indicators of changes in community structure, and by extension community stability.

Systematic changes in the slopes of M-N relationships have already been used to assess the state of marine fisheries ecosystems impacted by exploitation, terrestrial ecosystems affected by agriculture, and to understand the effects of warming on aquatic communities (Rice and Gislason 1996, Mulder and Elser 2009, Yvon-Durocher et al. 2011, O'Gorman et al. 2012). For example, fisheries impacted by size selective overfishing tend to have steeper slopes because the abundance of larger fish is decreased by fishing (Rice and Gislason 1996). The intercepts of M-N relationships have also been used to compare the structure of different communities (Boudreau and Dickie 1992, Cyr et al. 1997, Yvon-Durocher et al. 2011), with differences indicating alterations in abundance of species or individuals of the same body size. Moreover, systematic changes in the intercept of M-N relationships may reflect changes in ecosystem productivity (Boudreau and Dickie 1992, Cyr et al. 1997). Therefore, changes in the slope and intercept attributes of M-N relationships provide important insights into processes affecting community state, structure and stability. However, it is likely that other attributes of M-N relationships, such as the mass range, could also be developed and used to more accurately describe, compare and provide insight into drivers of community structure changes (Box 1).

Attributes of M-N relationships are likely to be particularly useful for evaluating the effects of process which influence the body size distribution of organisms or the productive base of food webs. Strong influences of these characteristics are likely bought about by alterations to habitat size and disturbance because habitat size ultimately constrains the body size of organisms that can live in a particular environment (Post et al. 2000, Jellyman et al. 2014), and disturbance affects resource production and abundance (Death 1996, Wootton et al. 1996). Understanding the effects of and mechanisms behind changes in both habitat size and disturbance on community structure is especially important for stream communities because current global changes are predicted to alter the amount of water in streams (habitat size) and

the magnitude of extreme events like floods (disturbance) (Christensen et al. 2013, Jones 2013). Therefore, changes in M-N attributes across gradients of habitat size and disturbance are likely to provide important insight into the mechanisms driving changes in communities across these gradients.

To investigate how well M-N relationships reflected changes in community structure associated with alterations in habitat size and disturbance, I constructed M-N relationships using the average body size and abundance of each species in 24 stream communities collected across habitat size and flooding disturbance gradients. I expected changes in community structure, associated with changes in habitat size, to be predominantly driven by changes to top predator body size, and therefore reflected in changes to attributes associated with the mass (M) axis. In contrast, I expected changes in community structure associated with changes in disturbance, to be largely driven by changes in the abundance of organisms, and therefore reflected in changes to attributes associated with the abundance (N) axis.

Box 1. Attributes of body mass-abundance relationships

The relationship between body mass (M) and abundance (N) typically plotted as log (M) against log (N) depicts the change in organism abundance with increasing mass (White et al. 2007). Trebilco et al. (2013) made the link between the slopes of M-N relationships and Eltonian ecological pyramids, demonstrating that M-N relationships and ecological pyramids are different graphical representations of the same data. Consequently, showing that changing the slope of the relationships between M and N results in different community structures (Trebilco et al. 2013). Importantly, this highlighted that M-N relationships are a particularly useful and relatively easy way to summarise the structure of different communities.

Although changes in the slopes of M-N relationships are useful indicators of changes in community structure, there are other attributes of M-N relationships that require no additional data collection and can provide a more complete picture of differences in community structure. I propose four attributes that characterise M-N relationships that can aid in the comparison or assessment of the state of different communities through space and time (Figure 1).

(1) *Slope*

Steeper M-N slopes reflect communities with relatively more abundant smaller organisms and fewer larger organisms compared to shallow slopes which represent communities with comparatively more large organisms, relative to small organisms (dotted and solid lines, respectively, in Figure 1e). Changes in the slope of M-N relationships will be reflected in changes to other M-N attributes.

(2 & 3) *Intercepts ($\widehat{N}_{min\ M}$ and $\widehat{N}_{max\ M}$)*

Generally, the M-N intercept studied has been for N when M is zero (but see, Yvon-Durocher et al. 2011, O'Gorman et al. 2012). However, estimating N for when M is zero is not always biologically meaningful, especially if it is not within the mass range being analysed. Additionally, if M=0 is not within the mass range of organisms being analysed, changes in community structure could go undetected. For example, the M-N slope could stay the same and the intercept at x=0 could stay the same, but the mass range of organisms in a community could change (decrease or increase) resulting in a different community structure (e.g. dotted and solid lines, respectively, in Figure 1d). This change would go undetected using just M-N slope and intercept. Therefore, I propose two intercept-related attributes of M-N relationships which should more accurately reflect community change: 1) the abundance predicted for the smallest organism/species/size class ($\widehat{N}_{\text{min M}}$), and 2) the abundance predicted for the largest organism/species/size class, $\widehat{N}_{\text{max M}}$ (Figure 1a). Changes in values of $\widehat{N}_{\text{min M}}$ indicate changes in the abundance of the smallest organisms or trophic levels in a community and changes in values of $\widehat{N}_{\text{max M}}$ indicate alterations in the abundance of the largest organisms or trophic levels in a community.

If both $\widehat{N}_{\text{min M}}$ and $\widehat{N}_{\text{max M}}$ increase or decrease by the same amount then there will be no change in the other M-N attributes (mass range and slope) and this will be reflected in an equal change in abundance across the entire mass range (e.g. change from dotted to solid line Figure 1c). Additionally, this should be reflected in an increase or decrease in the total biomass of the community. Alternatively, changes of different magnitude in either $\widehat{N}_{\text{min M}}$ or $\widehat{N}_{\text{max M}}$ provide information on which parts of the community are becoming more or less abundant and should also be reflected in changes to at least one other M-N attribute. For example, in Figure 1e, an increase in $\widehat{N}_{\text{max M}}$ compared to the reference condition (change

from dotted line to solid line), indicates an increase in abundance and biomass of the largest organisms in the community.

(4) *Mass Range*

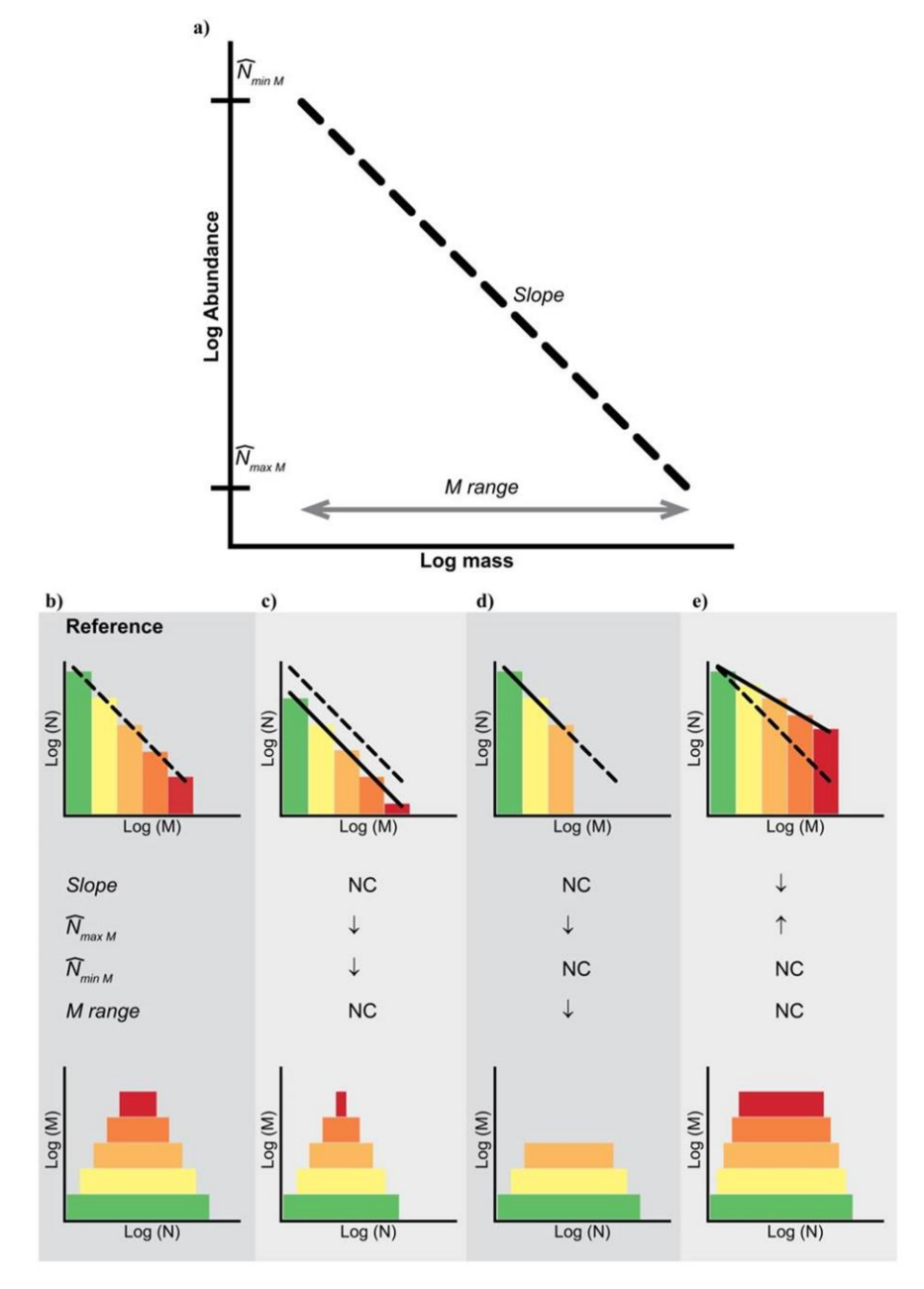
The mass range attribute provides information on the size range of organisms being used in the construction of the M-N relationship. Changes in mass range should indicate the addition or loss of small or large organisms from a community. Because body size is often related to trophic level, changes in the mass range attribute should also reflect changes to trophic pyramid height (e.g. Figure 1d).

All four attributes of M-N relationships are not independent, and therefore changes in community structure will be reflected in changes to more than one of the attributes at once. Although they are not independent, they allow a more complete understanding of what aspects of communities are changing and provide more insight into the mechanisms of these community changes.

Types of data

Relationships between M and N can be constructed using different types of data (see White et al., 2007, for review). For example, the cross-species or species-average approach shows the relationship between average mass and abundance for taxonomically defined groups in a community. Alternatively, the individual approach, often referred to as size spectra, involves grouping individuals into size based bins and summing the number of individuals in each bin as an estimate of abundance. Although individual size-based data may be better for testing ecological theory, and are the type of data used in linking M-N relationships and ecological pyramids (Trebilco et al. 2013), if the goal of using M-N relationships is to compare different communities, then species-averaged data still provide a very informative picture of the

relative structure of different communities. However, an accurate comparison of M-N attributes across different communities requires that the relationships are constructed in the same way. For example, species-average constructed M-N relationships must be compared with other species-average relationships, and not with individual based relationships and vice versa. Additionally, the use of the M-N attributes identified here does not need to be limited to only community data. The attributes could also be used to compare the size structuring of species or individuals within a single trophic level or for single species populations, for example to examine the size structure and recruitment success off a species across different gradients.



Box 1 Figure 1: Conceptual body mass-abundance (M-N) relationship showing (a) four M-N attributes and (b-e) examples demonstrating how comparing changes in the different M-N attributes over and above the slope can be used to understand changes in community structure represented as changes in Eltonian pyramids. The four attributes are the slope of the relationship between M and N (*Slope*), the predicted abundance for the smallest and largest organism/species/size class ($\widehat{N}_{min\ M}$ and $\widehat{N}_{max\ M}$, respectively), and the size range of organisms being used in the construction of the M-N relationship (*M range*). Different colours indicate how different trophic levels translate between M-N relationships and Eltonian pyramids. In panel b), and the dotted lines represent a reference M-N relationship which is used to compared changes in the M-N relationships and associated attributes in c-e (solid line). NC represents no change in the M-N attribute, up pointing arrow (↑) indicates an increase in the M-N attribute and a down pointing arrow (↓) indicates a decrease in the M-N attribute.

Methods

Dataset

I quantified M-N relationships using data from 24 stream communities from previously published (McHugh et al. 2014) and unpublished data collected from the Waimakariri and Rakaia River catchments, New Zealand (Table 1). The streams spanned large habitat size and disturbance gradients, were first to fourth order grassland streams, and were sampled using comparable quantitative methods in either the austral summer of 2004-2005 or 2009-2010. Sites sampled were 30-50 m long reaches selected to span a range of stream sizes (cross-sectional area: 0.14 m^2 to 4.52 m^2) (Table 1) and a gradient of flooding disturbance from stable spring-fed to highly flood prone mountain-fed rivers (Table 1). Only perennially–flowing streams with fish present were included in this analysis.

Stream physical characteristics

Habitat size was measured as average wetted cross-sectional area (m^2) of the sample reach, calculated as an average of the product of width and mean depth (n = 5 depth measurements per transect) over five transects along a 30-50 m sampling reach. The Pfankuch River Disturbance Index (RDI, Pfankuch 1975) was used to quantify the disturbance regime. This index is a subjective, score-based, assessment of 15 aspects of channel morphology, including stream bed and bank descriptors, and is strongly correlated with other quantitative measures of flooding disturbance affecting stream fish and invertebrates (Jellyman et al. 2013b, Peckarsky et al. 2014). Pearson's correlation showed no significant correlation between $\log_{10}$ habitat size and disturbance ($p=0.66$, $r=0.09$) across the 24 streams used in this study (Figure S2).

Table 1. Location (New Zealand map grid, NZMG), average stream size (cross-sectional area, CSA), and Pfankuch River Disturbance Index (RDI) for the sites included in this study.

Site name	NZMG Easting	Northing	CSA (m^2)	RDI
Acheron River	2402460	5763670	0.642	82
Andrews River	2411315	5800085	0.813	84
Antipodes	2402885	5763135	0.266	90
Broken River	2406520	5778765	2.091	110
Cass River	2408015	5797090	1.648	112
Coach Stream	2409200	5765985	0.232	98
Cooper	2438820	5767755	0.478	75
Craigieburn Cutting	2408175	5784305	0.188	124
Craigieburn Stream	2409640	5785225	0.672	81
Dry Spring	2405475	5771425	0.185	110
Dry Gorge	2406615	5770860	0.372	75
Grasmere Stream	2408765	5796365	1.182	68
Helm	2402620	5762215	0.292	89
Little Kowai	2423265	5765255	0.278	91
Lower farm Stream	2412835	5799840	0.597	84
Mansons Creek	2409635	5785435	0.366	58
One Tree Swamp	2406440	5800130	4.144	66
Pass	2406590	5767415	0.138	104
Porter River	2406955	5773080	3.183	96
Pudding Hill	2392245	5732895	0.495	87
Slip Spring	2405145	5771525	0.794	69
Waimakariri River	2410715	5799300	4.466	137
Waimakariri Spring	2413500	5798075	1.146	82

Invertebrate and fish communities

Marcroinvertebrates were sampled at three to five locations in each stream site using a Surber sampler (25 × 25 cm, 300 μm mesh), preserved in ethanol and separated from detritus under a dissecting microscope. Taxa were enumerated and identified to the lowest possible level, mostly genus, using appropriate keys (Winterbourn et al. 2000). Dry mass was calculated (not including cases and shells) using established length-weight regressions on representative samples of individuals (McHugh et al. 2014).

Fish communities were sampled using electrofishing over a 30 m reach using two methods. Either the upper and lower ends of the 30 m reach were blocked with nets, and three successive electrofishing depletion passes were conducted to remove as many fish as possible and a depletion estimator was used to estimate fish density (McHugh et al. 2010) oralternatively, the lower end of each sampling reach was blocked with a net and a single upstream-to-downstream electrofishing pass was made to remove as many fish as possible with dip nets (McHugh et al. 2014). Single-pass catches were converted to equivalent population estimates based on species-specific one pass vs. total abundance relationships estimated from electrofishing surveys conducted previously in the study area (McHugh et al. 2014). Additionally, at the time of sampling the study reaches of large rivers were also monitored to determine the presence of individual large fish which were difficult to capture during standard electrofishing. In two cases large fish (trout > 300 mm fork length) were present in the study reach and were captured in a separate electrofishing effort specifically targeting them. Abundance estimates for these fish have been adjusted to account for the larger sampling area. The lengths of each fish were converted to dry weights using length–dry weight relationships (Jellyman et al. 2013a).

Statistical analyses

Body mass-abundance (M-N) relationships were constructed for the communities in each stream by plotting the $\log_{10}$ transformed average dry mass of each species against their population density, analogous to the local size density distribution described by White et al. (2007). Linear regression was used to determine the relationship between log-transformed M and N in each community and the four M-N attributes: (1) *slope*, the slope of the relationship between M and N; (2) $\widehat{N}_{min\ M,}$ the predicted abundance for the smallest organism; (3) $\widehat{N}_{max\ M}$,

the predicted abundance for the largest organism; (4) *M range*, the size range of organisms being used in the construction of the M-N relationship (Box 1).

Because the four attributes of the M-N relationships are not independent, multivariate analysis of variance (MANOVA) was initially used to test for significant changes across the habitat size and disturbance gradients. Significant effects in the MANOVA were further tested using separate protected univariate multiple regression analyses between the individual attributes (Scheiner 1993). Non-significant interactions in the MANOVA were excluded from the univariate analyses. Similarly, MANOVA was used to test changes in abundance, biomass and predator-prey ratios across the size and disturbance gradient further tested by independent multiple regressions. In all analyses both habitat size and disturbance were included as continuous predictors and habitat size was $\log_{10}$ transformed to improve homogeneity of variances and linearity. All statistical analyses were carried out in R 3.1.2 (R Core Team 2015)

Results

In general, there was a negative relationship between the body size (M) and abundance (N) of organisms within each of the 24 communities studied (for raw M-N relationships see Figure S1). The slope coefficients for these relationships varied between -0.22 and -0.99 and systematic changes in community structure associated with both the habitat size and disturbance gradients were reflected in changes to all four attributes (slope, $\widehat{N}_{\text{max M}}$, $\widehat{N}_{\text{max M}}$, and mass range) of the M-N relationships (Table 2, Figure 1). Only the independent main effects of habitat size and disturbance were included in the univariate ANOVAs because the

MANOVA analyses indicated that there were no significant interactions between habitat size and disturbance (Table 2).

Habitat size

The independent effect of habitat size on the M-N slope of each community was negative, with M-N slopes becoming significantly steeper/more negative with increasing habitat size (Table 2, Figure 1a). In contrast, there was no effect of habitat size on the $\widehat{N}_{\text{min M}}$ attribute (Table 2, Figure 1c). However, as stream size increased the predicted abundance of the largest organism in a community ($\widehat{N}_{\text{max M}}$) decreased from 3.86 m^{-2} to 0.006 m^{-2} (Table 2, Figure 1d). Mass range was also affected by stream size (Table 2, Figure 1g); the mass range of organisms in a community increased from 0.331 g to 110.45 g as stream size increased. These changes in M-N attributes were reflected in a significant decrease in both the total abundance of individuals and a decrease in the ratio of the abundance of predators relative to prey with increasing habitat size (Table 3). In contrast, with increasing habitat size there was no change in the total community biomass or the biomass of predators relative to prey (Table 3).

Disturbance

The independent effect of disturbance on M-N slope was also negative (Figure 1b); as habitats became more disturbed, the M-N slope became significantly more negative (Figure 1b). There was also a negative relationship between disturbance and both the $\widehat{N}_{\text{min M}}$ and $\widehat{N}_{\text{max M}}$ attributes (Figure 1d & f). However, in contrast there was no effect of increasing disturbance on the mass range attribute (Figure 1g). These changes in the M-N attributes across the disturbance gradient were reflected in decreases in the abundance and also a decrease in the biomass of organisms from 14.21 $g.m^{-2}$ to 0.90 $g.m^{-2}$ with increasing

disturbance (Table 3, Figure 3). Similarly, both the abundance and predator to prey biomass ratios decreased with increasing disturbance (Table 3, Figure 3).

Table 2. Multivariate analyses of variance and univariate multiple regression results for the effects of habitat size (log_{10} CSA) and disturbance (RDI) on the four attributes (slope, $\widehat{N}_{\text{min M}}$, $\widehat{N}_{\text{max M}}$, mass range) of the body size-abundance relationship. See Box 1 for definitions of the four attributes. Degrees of freedom (d.f.), sums of squares (SS), F-value (F) and p-value (P) are all shown.

	d.f.	SS	F	P
MANOVA				
Log_{10} CSA	4,17	0.232	14.06	< 0.001[a]
RDI	4,17	0.321	8.98	< 0.001[a]
CSA*RDI	4,17	0.729	1.58	0.224[a]
Slope				
Log_{10} CSA	1	0.351	46.98	< 0.001
RDI	1	0.169	17.83	< 0.001
Residual	21	0.199		
$\widehat{N}_{\text{min M}}$				
Log_{10} CSA	1	0.002	0.02	0.728
RDI	1	0.452	4.12	0.055
Residual	21	2.309		
$\widehat{N}_{\text{max M}}$				
Log_{10} CSA	1	11.350	48.40	< 0.001
RDI	1	4.825	20.58	< 0.001
Residual	21	0.2345		
Log_{10} Range				
Log_{10} CSA	1	2.465	7.36	0.013
RDI	1	0.009	0.03	0.874
Residual	21	7.034		

[a] Wilks' Lambda

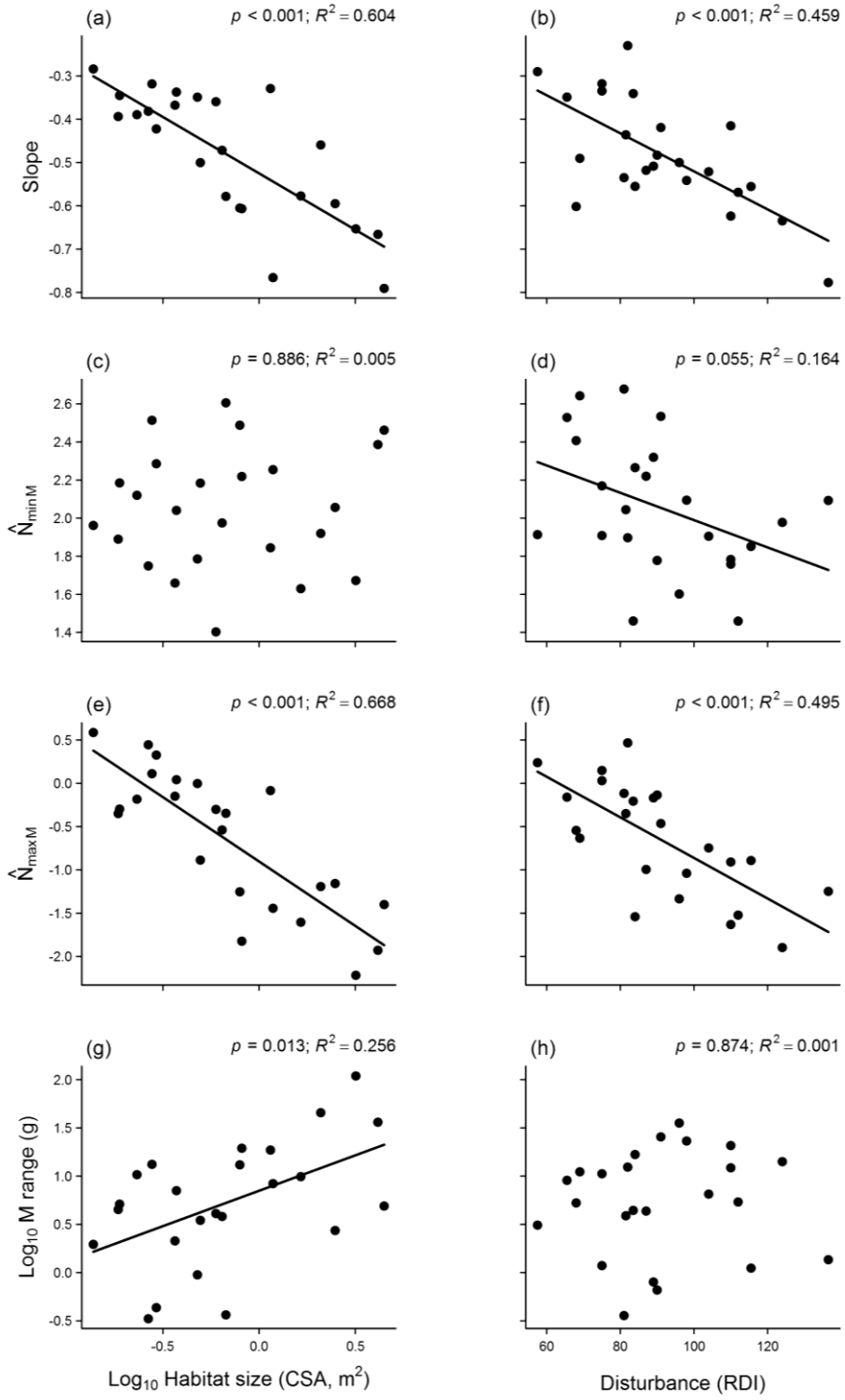


Figure 1. Relationships between the four attributes of the body size-abundance (M-N) relationship (see Box 1 for definitions), and habitat size (log_{10} cross-sectional area, CSA) and disturbance (river disturbance index, RDI). The relationships between habitat size and the four M-N attributes are plotted at the mean of disturbance to represent the independent effects of habitat size. Equivalently, the plots of disturbance against the four M-N attributes are plotted at the mean of habitat size to represent the independent effects of disturbance. The R^2 values represent the partial R^2 values and the p-values are the p-values associated with each independent main effect from multiple regression analysis.

Table 3. Multivariate analyses of variance and univariate multiple regression results for the effects of habitat size (log_{10} CSA) and disturbance (RDI) on the total number of individuals in a community (Abundance, density m^{-2}), total community biomass ($g.m^{-2}$), the ratio between the number of predators relative to prey in a community (N pred: prey) and the ratio between the biomass of predators relative to prey (MN pred:prey), where N is abundance and MN is biomass. Degrees of freedom (d.f.), sums of squares (SS), F-value (F) and p-value (P) are all shown.

	d.f.	SS	F	P
MANOVA				
Log_{10} CSA	2,19	0.706	3.95	<0.037[a]
RDI	2,19	0.715	3.79	<0.041 [a]
CSA*RDI	2,19	0.799	2.39	0.119 [a]
Abundance				
Log_{10} CSA	1	0.442	8.07	0.010
RDI	1	0.733	13.38	0.001
Residual	21	1.150		
Biomass				
Log_{10} CSA	1	0.069	1.18	0.289
RDI	1	0.751	12.91	0.002
Residual	21	1.222		
Npred:prey				
Log_{10} CSA	1	0.902	7.76	0.011
RDI	1	0.610	5.25	0.032
Residual	21	2.44		
MNpred:prey				
Log_{10} CSA	1	0.011	0.06	0.810
RDI	1	0.624	3.51	0.075
Residual	21	3.729		

[a] Wilks' Lambda

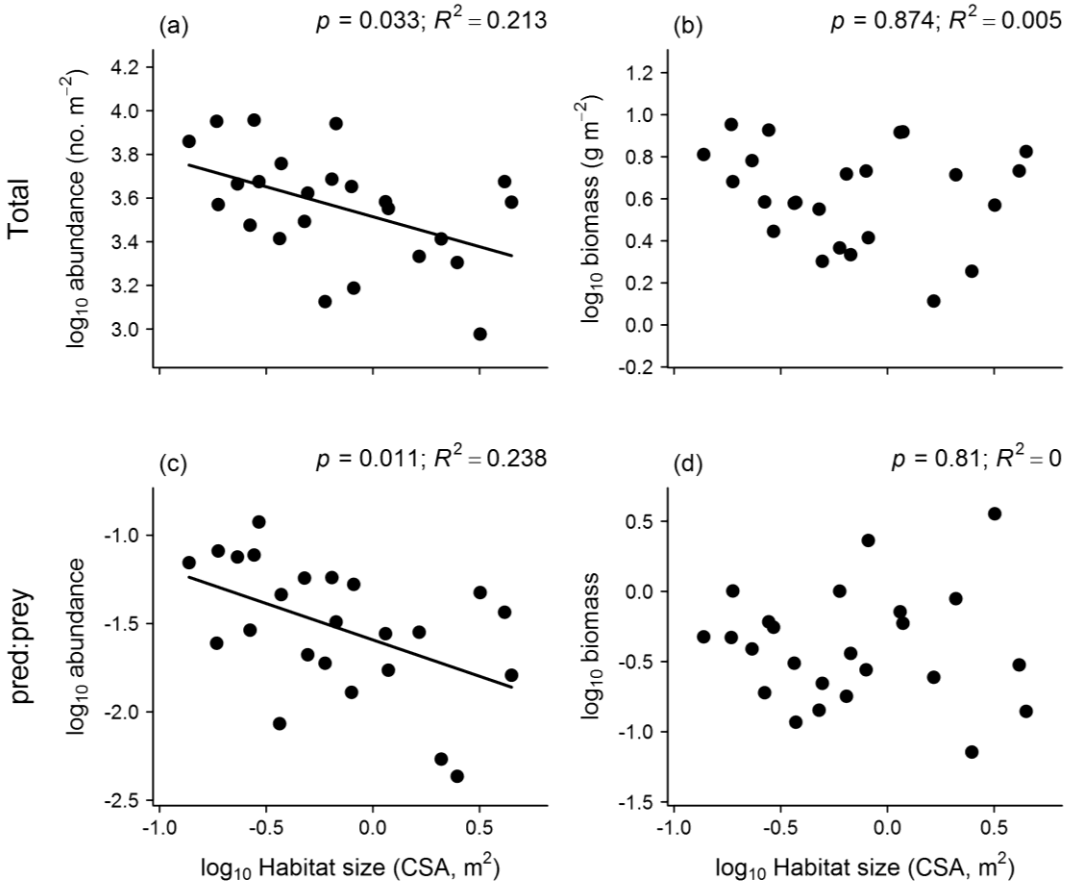


Figure 2. Relationships between $\log_{10}$ habitat size measured as cross sectional area (CSA) and the total number of individuals in each community (a), total community biomass (b), the abundance of predators relative to the abundance of prey (c), and the biomass of predators relative to the biomass of prey (d). All responses are plotted at the mean of disturbance to represent the independent effects of habitat size. The R^2 values represent the partial R^2 values and the p-values are the p-values associated with each independent main effect from multiple regression analysis**.**

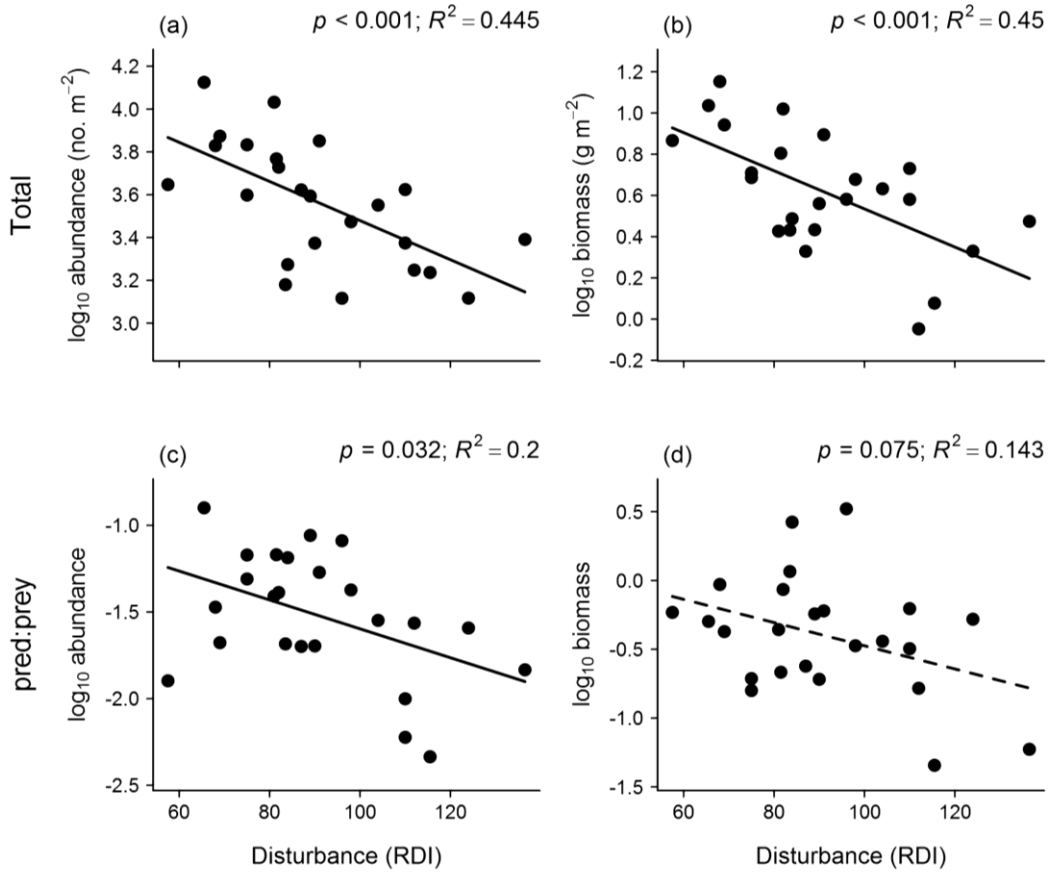


Figure 3. Relationships between disturbance measured by the Pfankuch River Disturbance Index (RDI) and the total number of individuals in each community (a), total community biomass (b), the abundance of predators relative to the abundance of prey (c), and the biomass of predators relative to the biomass of prey (d). All plots are plotted at the mean of habitat size to best represent the independent effects of disturbance. The R^2 values represent the partial R^2 values and the p-values are the p-values associated with each independent main effect from multiple regression analysis.

Discussion

Developing metrics that can reliably summarise the structural properties of ecological networks will help improve our understanding of drivers of community change and provide potentially useful tools for monitoring the response of communities to ongoing or future perturbations. I have shown that a novel method for quantifying community structure detected important changes across ecological gradients of habitat size and disturbance (Figure 4), indicating that both habitat size and disturbance are major axes of community change. Specifically, changes in the slopes of M-N relationships, in addition to other M-N attributes which required no extra data collection, highlighted that changes associated with habitat size were largely driven by changes in predator body mass, whereas changes in disturbance were mainly driven by changes in abundance across the community.

Habitat size

Community structure changed systematically across the habitat size gradient, indicated by the increasingly negative relationship between M and N with increasing habitat size. Other attributes of the M-N relationship ($\widehat{N}_{\min M}$, $\widehat{N}_{\max M}$, mass range) revealed that these changes in slope (community structure) were driven by changes in the size and abundance of the largest organisms in each community, while abundance of the smallest organisms did not change (Figure 4). As habitat size increased, the size of species in the community also increased, indicated by a positive relationship between the mass range attribute and habitat size. Due to their greater body size, large top predators have bigger home ranges and higher resource requirements and thus, require larger habitat sizes (Minns 1995, Jetz et al. 2004, Jellyman et al. 2014). Therefore, changes in M-N relationships across a habitat size gradient are indicative of the constraints habitat size places on the size of top predators.

Larger habitats also support communities with longer food chains (e.g. Post et al. 2000, McHugh et al. 2010) which would indicate "taller" Eltonian pyramids. Body size is often closely linked to trophic position, with larger organisms, generally predators, positioned higher up the food chain (Jennings et al. 2001, Arim et al. 2010, Riede et al. 2011). Therefore, an increase in the mass range of a community should be linked to changes in food chain length. Consequently, our results support the hypothesis of longer food chains in larger habitats, as indicated by increases in the mass range attribute.

Although larger organisms were found in larger habitats, they were found at a lower abundance. This change in abundance of larger organisms was highlighted by a decrease in the $\widehat{N}_{\max(M)}$ attribute with increasing habitat size (Figure 4). In comparison, there was no change in the $\widehat{N}_{\min(M)}$ attribute with changes in habitat size, indicating that the abundance of small organisms was not affected by habitat size. Therefore, these changes in the M-N attributes reveal that habitat size mainly drives changes in community structure through its influence on the top of food chains.

Patterns in the M-N attributes were also connected to changes in more coarsely resolved community properties such as total abundance, biomass and the ratio of predators relative to prey. Across the habitat size gradient, both total abundance and the ratio of the number of predators relative to prey decreased. However, there was no change in the total community biomass or the ratio of predator biomass to prey biomass. Therefore, the increased size and decreased abundance of the biggest organisms in large habitats was countered by an increased abundance of the biggest organisms in smaller habitats, but with those biggest organisms being comparatively smaller (Figure 4). Changes in these coarse community properties also corresponded with changes in the $\widehat{N}_{\min M}$ and $\widehat{N}_{\max M}$ and mass range attributes,

highlighting that more than just M-N slopes were required to tease apart community structure changes.

The amount of energy available to large organisms in a community is thought to partially control the slopes of M-N relationships (Jennings 2005, Trebilco et al. 2013). The lack of change in the $\widehat{N}_{\text{min M}}$ attribute across the habitat size gradient indicates that there was a constant amount of prey resource per unit area available to support larger predatory organisms regardless of habitat size. Consequently, the lack of change in the biomass of predators relative to prey across the habitat size gradient indicates that, for the same amount of prey biomass, a habitat can either support more smaller predators, or fewer larger predators. Therefore, it appears a main influence of habitat size on community structure is to limit the size of large organisms, with the abundance of those larger organisms subsequently constrained by the amount of energy available to them.

Disturbance

Changes in habitat disturbance altered community structure predominantly through changes in abundance, revealed by the $\widehat{N}_{\text{min M}}$ and $\widehat{N}_{\text{max M}}$ M-N attributes (Figure 4). Both $\widehat{N}_{\text{min M}}$ and $\widehat{N}_{\text{max M}}$ systematically decreased with increasing disturbance, indicating a decrease in the abundance of the smallest and largest organisms in the community (Figure 4). However, with increased disturbance the abundance of larger organisms decreased disproportionately more compared to small organisms, resulting in steeper M-N slopes (Figure 4). Larger organisms are disproportionately affected by disturbances (Estes et al. 2011, Jellyman et al. 2013b, Jellyman et al. 2014), but the changes in M-N attributes indicate that it was their abundance that was decreased by disturbance rather than their maximum body size because there was no change in the size range attribute across the disturbance gradient (Figure 4). Thus, unlike

habitat size, disturbance did not appear to constrain the size of the largest organisms, only their abundance.

The changes in the M-N attributes across the disturbance gradient also indicated differences in community structures which should be reflected in changes to more coarsely resolved community properties. As habitats became more disturbed, the abundance of both small and large organisms was decreased moving the whole M-N relationship line down (Figure 4). This change in the M-N relationships was reflected in decreases in both the total community abundance and biomass with increasing disturbance. The $\widehat{N}_{\max M}$ attribute decreased more with increasing disturbance than $\widehat{N}_{\min M}$, and there was no compensatory change in mass range like there was with changes in habitat size. Therefore, these changes, and the overall steeper slope of the M-N relationship, indicate a decrease in the number and biomass of the largest and smallest size classes in each community. As expected, the numbers of predators relative to prey decreased with increasing disturbance, and there was a statistically weaker negative relationship between disturbance and the ratio of predator biomass to prey biomass. Therefore, M-N attributes indicate the specific components of community change with disturbance, revealing how the effects of disturbance were propagated throughout communities.

Implications

The changes in community structure highlighted by changes in the M-N attributes and supported by changes in coarse community properties, will possibly also reflect changes in both the stability and functioning of ecosystems. For example, both small habitats and more benign (i.e. less disturbed) habitats had shallower M-N slopes and relatively more predators relative to prey. Therefore, these communities are likely to be characterised by stronger predator-prey interactions. The distribution of interaction strengths in a community can

determine its stability (resistance and resilience to perturbations) (de Ruiter et al. 1995, McCann et al. 1998, Neutel et al. 2002). Specifically, communities are likely to be more stable if they have relatively few strong interactions and many weak interactions (McCann et al. 1998, Emmerson and Raffaelli 2004). Therefore, although the communities included in this study are adapted for living in their current conditions, I would expect them to have different capacities to respond to future disturbances. For example, because small benign habitats have more predators relative to prey, their communities are more likely to be affected by further perturbations (i.e. less stable), compared to those living in large, disturbed habitats.

Overall, my findings highlight that both habitat size and disturbance are strong drivers of community structure, and that each places different pressures on communities. These differences were revealed using M-N relationships and in particular, the addition of the M-N attributes $\widehat{N}_{\text{min M}}$, $\widehat{N}_{\text{max M}}$ and mass range, over and above M-N slope, added important additional information about community structure. Therefore, using M-N relationships and their associated attributes provides a promising way of easily and accurately assessing, monitoring and comparing different community structures.

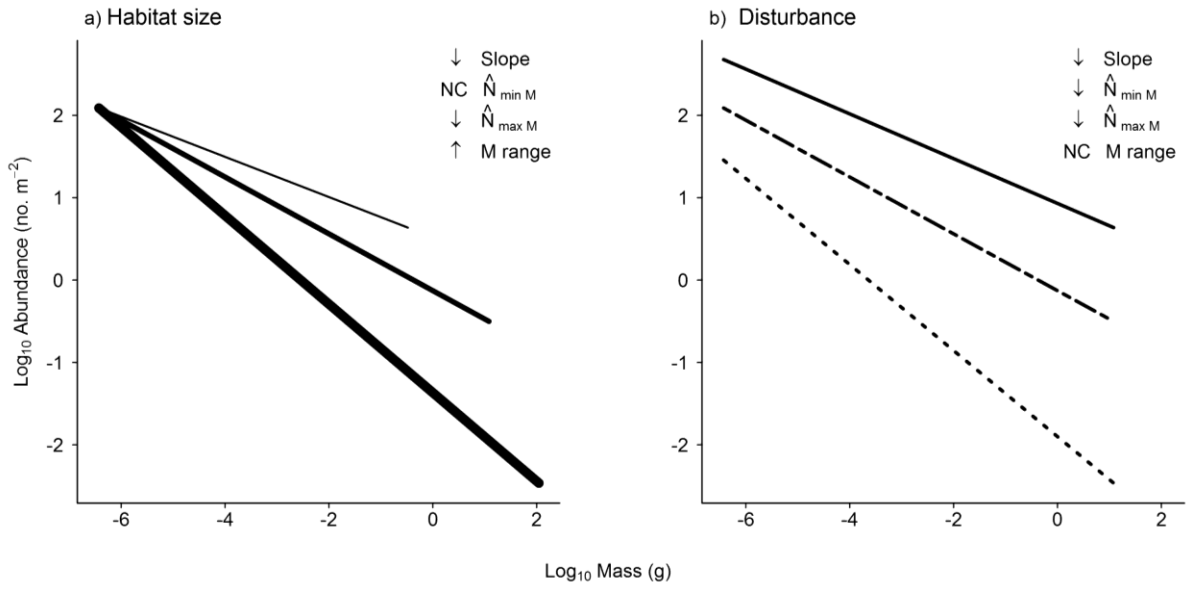


Figure 4. Summary plots showing the effects of decreasing habitat size (a, reduction in line width) and increases in disturbance (b, solid to dashed, then to dotted lines) on the body size-abundance (M-N) relationships from 24 streams used in this study. The lines of both plots are based on regression lines from the M-N relationships of the communities analysed in this study. The three habitat size lines (a) represent the smallest (thinnest line), average and largest sized (thick line) habitats. The three disturbance lines (b) represent the most stable (solid line), average (dashed line), and most disturbed stream (dotted line). The M-N relationships were corrected for the effects of disturbance and stream size in (a) and (b), respectively. The arrows next to each of the four M-N attributes in each plot represent an increase/positive relationships (↑) a negative relationship (↓) or a non-significant (NC) relationship between each of the M-N attributes (see Box 1 for definitions) and increasing stream size or increasing disturbance.

Supplementary material

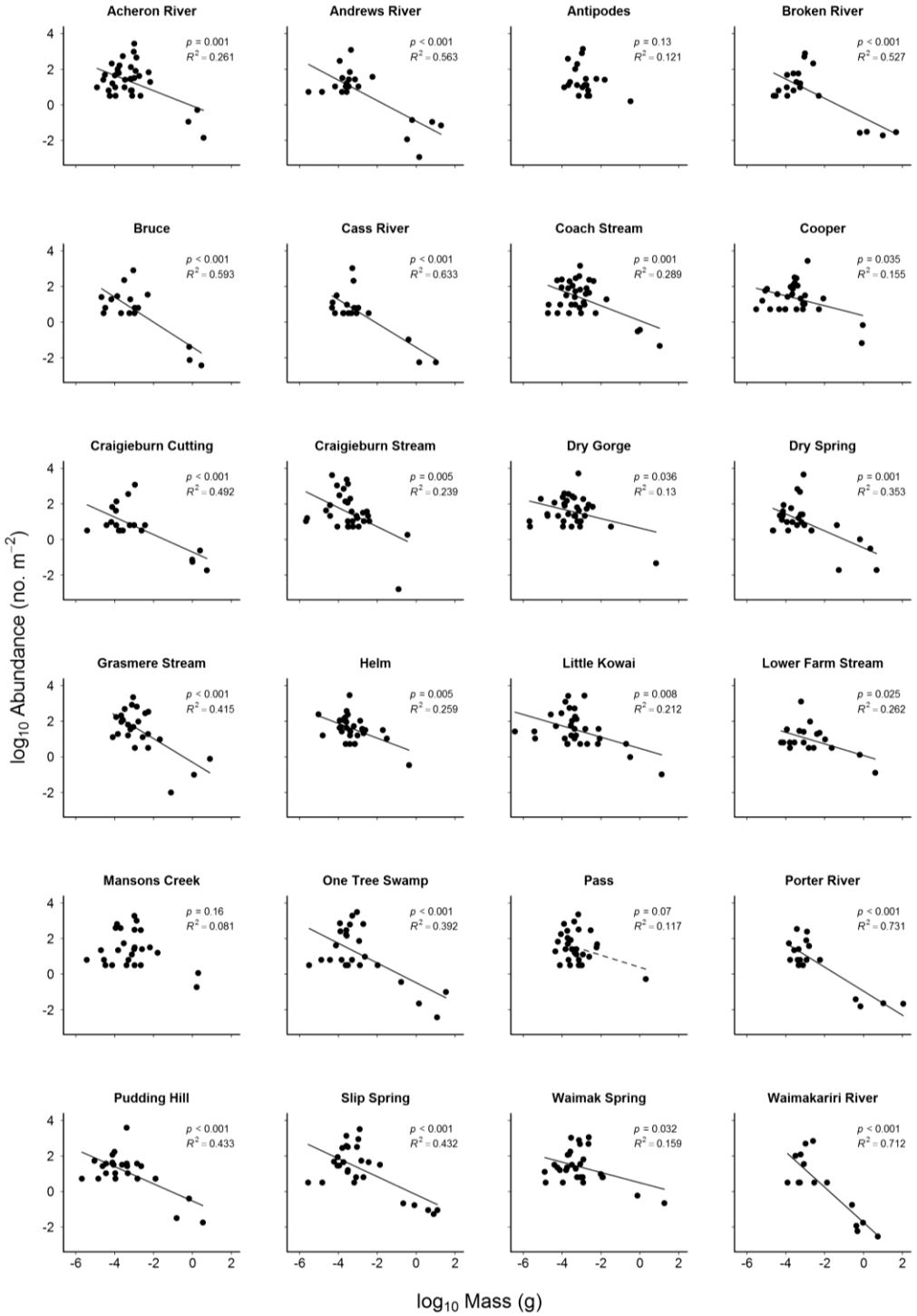


Figure S1. The relationship between $\log_{10}$ mass and $\log_{10}$ abundance for the 24 streams included in this study. Each point on each graph represents a unique taxa group. The p-values are generated from regression analysis and R^2 is the multiple R^2 value.

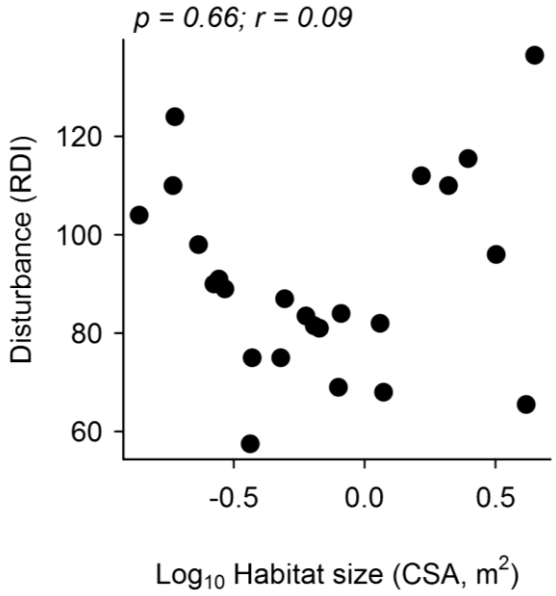


Figure S2. Scatter plot showing no significant correlation between $\log_{10}$ cross sectional area (CSA) and the Pfankuch River Disturbance Index (RDI) for each of the 24 streams used in this study. The p-value and r from Pearson's correlation analysis are shown.

Chapter Three

Prey defences modify the relationship between body size and interaction strength

Introduction

Predator-prey interactions are a key force driving the structure and dynamics of ecological communities (Barbosa and Castellanos 2005). Interaction strengths estimate the magnitude of predator effects on their prey, and the relative distribution of weak and strong interactions in a community can affect both community stability and function (McCann et al. 1998, Neutel et al. 2002, Tylianakis et al. 2007, Woodward 2009). Both theoretical and empirical studies indicate that communities are generally more stable (resistant and resilient to perturbations) when there are many weak and only a few strong predator-prey interactions (de Ruiter et al. 1995, McCann et al. 1998, Neutel et al. 2002, Emmerson and Raffaelli 2004). Therefore, determining the factors controlling the relative strengths of predator-prey interactions in food webs is important for characterising community stability and understanding communities' responses to perturbations.

Despite their importance, measuring the strengths of all predator-prey interactions in a community is logistically challenging given the complex nature of most communities (Morales-Castilla et al. 2015). Consequently, recent efforts have focused on identifying drivers of interaction strength and developing reliable proxy interaction strength measures that can be used to estimate the strength of interactions in complex communities (Emmerson and Raffaelli 2004, Brose et al. 2008, Morales-Castilla et al. 2015). Significantly, body size is related to a suite of traits (e.g. gape size) and processes (e.g. encounter and attack rates and

handling times) which are important in the predation process and may ultimately determine the strength of predator-prey interactions (Woodward and Warren 2007, Brose et al. 2008). Thus, both theoretical and empirical studies suggest that there should be predictable allometric scaling relationships between body size and interaction strengths largely based on metabolic scaling theory (Brown et al. 2004, Emmerson et al. 2005, Brose et al. 2008, Schmitz and Price 2011). Therefore, body size is a promising proxy variable for estimating the interactions strengths in food webs. For example, Emmerson and Raffaelli (2004) empirically showed that per capita interaction strengths had a positive power-scaling relationship with predator-prey body mass ratios (PPMR). Their study reported a scaling exponent not significantly different from 0.75 and the scaling exponent from their study has subsequently been used to parameterise the strength of interactions in food web models underpinning studies of the role of interaction strengths in food web stability (e.g. Reuman and Cohen 2005, Montoya et al. 2009, Layer et al. 2010).

Although body size is likely to be a fundamental trait driving the strength of interactions in communities, these interaction strength relationships have been developed from a limited set of communities, and empirical tests of their generality are rare. Moreover it is likely that in addition to body size, other traits of species performance such as predator foraging mode and prey vulnerability also influence predator-prey interaction strength (Rossberg et al. 2010, Rall et al. 2011, Klecka and Boukal 2013, Boukal 2014). For example, Klecka and Boukal (2013) demonstrated experimentally that in addition to body size, predators with different foraging traits and prey varying in vulnerability (measured as microhabitat use, feeding mode and escape behaviour), modified the strength of interactions. Consequently, PPMRs may set the potential upper limits for interaction strengths but other traits may also determine the realised interaction strengths within these limits, and therefore be important for improving the estimation of interaction strengths within communities.

Morphological defences, such as cases, shells and spines, which are common in freshwater animals, can modify predator-prey interactions by making prey less vulnerable to predators (Wootton et al. 1996, Mikolajewski and Rolff 2004, Ferry et al. 2013). Therefore, for a given PPMR, it is likely that an undefended prey (i.e. without morphological defences) would be preyed on more than a defended prey (i.e. with morphological defences). I tested the generality of the relationship between interaction strengths and PPMR, and evaluated how morphological defences affected this relationship, through a series of stream mesocosm experiments with predator species spanning four orders of magnitude in mass and both undefended and defended prey species. I predicted that interaction strengths would increase with increasing PPMRs, but the presence of morphological defences would significantly lower interaction strengths and therefore alter the relationship between PPMR and interaction strength.

Methods

To investigate the relationship between PPMRs and interaction strengths, I ran experiments in stream mesocosms using both predatory invertebrates and fish, and a range of defended and undefended prey species from streams in Canterbury, New Zealand.

Mesocosms

Circular basins (52 cm wide) were used to create flow-through mesocosms designed to replicate a stream environment (Figure 1). Mesocosms were set up inside a shed adjacent to a perennially flowing stream. Water was pumped into the shed, filtered, pumped around tanks and then drained back out into the stream. Water flow (0.04 ± 0.0005 $m.s^{-1}$) was created by two water jets facing in opposite directions on each side of a mesh-covered central standpipe (3 cm wide) that controlled water depth (12.5 cm). Each mesocosm base was painted with

non-toxic pond paint mixed with sand to create a rough surface suitable for aquatic invertebrates to walk on, and terracotta saucers and pots were added for fish and invertebrate cover (Figure 1). Terracotta substrates were colonised with algae prior to each experiment to provide a food source for invertebrates, and were exchanged after each experimental round. Mesocosms were also covered in a mesh lid to prevent fish escape. A maximum of 36 mesocosms (trials) were run in any experimental round. Light conditions were standardised using a 12-hour light-dark period.

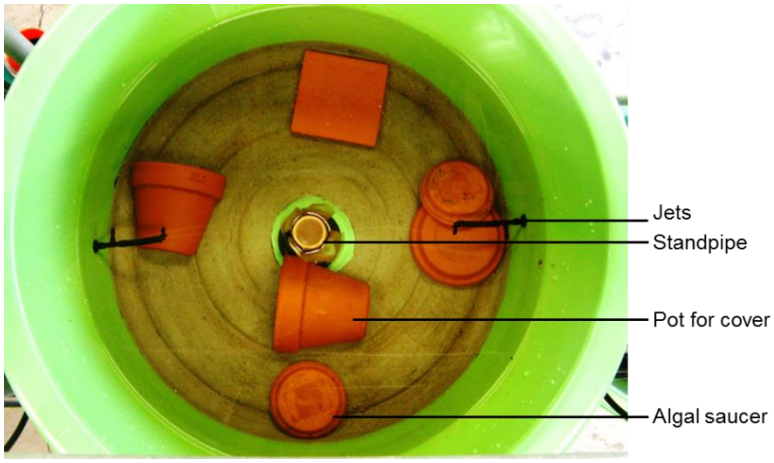


Figure 1. Mesocosm set-up, with terracotta pots and saucers for fish cover and algal growth surfaces, jets generating circular flow around the tank (52 cm wide), and the stand pipe (3 cm wide) maintaining water depth (12.5 cm).

Experimental design

The experiment was carried out over different days and years for a total of 286 different predator-prey species combinations (Table S 1). The predator-prey combinations were arranged into multiple experimental rounds (one 24 hour experiment period, a maximum of 36 mesocosms), each involving multiple trials (a single meocosms containing a single predator-prey pairing). Four different predators and six different prey forming common links in local stream food webs were used. Predator species were selected to represent a natural size gradient and included both predatory invertebrates and fish (Table S 2). In addition to

evaluating a natural body size gradient across predator species, the experiment was also designed to test the relationships between predator size and interaction strength within each predator species. Therefore, a gradient of sizes from smaller to larger individuals was collected for each predator species (see Table S 2 for the predator size range used in experiments). One predatory invertebrate (*Archicauliodes diversus*, dobsonfly) and two predatory fish (*Galaxias vulgaris* and *Salmo trutta*) were used in 2011, and an additional invertebrate predator, *Stenoperla prasina* (stonefly), was included in 2012.

Prey taxa were selected to include both undefended and morphologically-defended prey which had a case, shell or spines. In 2011, two undefended mayfly taxa, *Deleatidium* sp. and *Nesameletus ornatus*, and two morphologically defended prey, the cased caddisfly *Olinga* sp. and the snail, *Potamopyrgus antipodarum* were used in experiments. Additional prey taxa, a defended cased caddisfly (*Pycnocentrodes* sp.) and a defended spiny-gilled mayfly (*Coloburiscus humeralis*) were used in 2012. Prey sizes were selected to be as uniform as possible within each taxa (see Table S 2 for the prey sizes). Animals were sourced from local streams and rocky lake shores using a combination of electrofishing/bugging, kick net and cobble-sampling techniques.

Predators were collected the day prior to an experimental round and left in the mesocosms (one per mesocosm) overnight prior to prey being added. Thirty and 50 prey per mesocosm were used in 2011 and 2012, respectively. These numbers per mesocosm are representative of densities of these prey found in surrounding streams (Table S 3). Prey species were randomly assigned to rounds and trials within rounds, until all combinations had been completed within each year. Every predator species and size range was used in each experimental round. After prey were added to mesocosms, experiments were left to run for approximately 24 hours, where after predators were removed, and remaining prey were counted out of the mesocosms.

In each experimental round at least one control trial (no predator added) for each prey taxa being used was run, and control trials from each round were combined and used to adjust for counting errors and to calculate prey dry weights. The dry weights of predators and prey were calculated from length-weight regressions (Table S 2) and were used to calculate biomass. Invertebrate predator and prey lengths were measured post-experiment from preserved animals, whereas fish lengths were measured prior. Any experimental mesocosms in which invertebrate predators moulted or fish did not acclimate were removed from the final analyses.

Statistical analysis

Per capita interaction strengths were calculated using the dynamic index, also known as the log-ratio method (Berlow et al. 1999, Berlow et al. 2004), which was the same interaction strength measure used by Emmerson and Raffaelli (2004):

$$Interaction\ strength_{(dynamic\ index)} = \frac{\log\left(\frac{P}{C}\right)}{Xt} \qquad \text{(Equation 1)}$$

where *P* was abundance of prey in the presence of predators, *C* was abundance of prey in the absence of predators which was calculated using all the control trials for each prey species in each year. *X* was abundance of predators, and *t* was the time period over which the experiment was run (hours). Trials in which no prey or all prey were eaten (only occurred in 1 trial) were removed from analyses due to constraints of the logarithm transformation and artifacts in results created by adding constants to zero values. A binomial generalised linear model (glm) using the canonical logit link function, analogous to a chi-square test of a contingency table, was used to test if the frequency trials without prey eaten differed between four broad predator-prey categories (predatory invertebrates-defended prey, predatory

invertebrates-undefended prey, predatory fish-defended prey and predatory fish-undefended prey).

The removal of some treatment combinations, and the different species of predators and prey used in 2011 and 2012 resulted in an unbalanced design. Consequently, all subsequent analyses were based on type III sums of squares where the significance of each term was only tested when last in the model.

Quantile regression (95^{th} quantile) was used to test for an overall limit relationship between the $\log_{10}$ ratio of predator size (g) to prey size (g), hereafter referred to as predator-prey mass ratio (PPMR), and $\log_{10}$ interaction strength using all 286 predator-prey pairs. Year was included in the initial model, but was not significant, so was subsequently removed. Linear models were used to investigate how the relationship between $\log_{10}$ PPMR and $\log_{10}$ interaction strength varied between defended and undefended prey using all predator-prey pairs, and then predatory invertebrates and predatory fish, respectively. Prey defence (defended or undefended) was included as a factor in models and year was included to control for density, predator species and prey changes across years which cannot be separated. Additional linear regressions were used to test the relationship between $\log_{10}$ PPMR and $\log_{10}$ consumption rate for each individual predator-prey pairing. Both PPMR and interaction strength were log-transformed to improve homogeneity of variances.

The amount of prey biomass eaten per hour divided by the predator biomass was used to calculate a mass-specific interaction strength for treatments in which at least one successful predation event occurred (see bracketed values in Table S 1 for treatment combinations). A linear model was used to investigate relationships between mass-specific interaction strength (measured as consumption rate) and $\log_{10}$ PPMR, prey defence, year and their associated two- and three-way interactions. Because of possible "spurious" correlations caused by the

shared term “predator mass” in both the denominator of the response variable (biomass eaten/predator mass) and the predictor (predator mass), permutation tests (similar to Hall et al. 2007) were used to test the significance of the relationship between mass specific interaction strength and the predictors mentioned above. Year was not significant in any of the mass-specific interaction strength permutation analyses, so was removed from subsequent models. In these permutation tests, the regression variable with no shared variance, “biomass eaten” was resampled with replacement 9999 times within each level of prey defence while keeping the shared variable “predator mass”, constant. The 9999 resampled response ratio datasets were then used in linear models with $\log_{10}$ predator mass and prey defence as the predictors. The expected F-values for each term in the linear model were estimated as the average of the F-values generated using the resampled response ratios. The p-values for permutated results were calculated for each term in the model as a tally of the number of resampled analyses producing an absolute difference from the expected F-value, that was larger than the absolute difference between the observed F-value (F-value using the original data) and the expected F-value (Hall et al. 2007). All analyses were carried out in R 3.1.2 (R Core Team 2015).

Results

Out of 286 predator-prey combinations, no prey were eaten in 106 (Table S 1). Predator type (invertebrate, fish) and prey type (defended, undefended) had significant effects on proportions of trials in which no prey were eaten (Figure 2, Table S 4). There were fewer zeros (i.e. no prey eaten) when both predatory fish and invertebrates were paired with undefended prey, and predatory fish paired with undefended prey had the smallest number of zeros (only 2 out of 64, Figure 2).

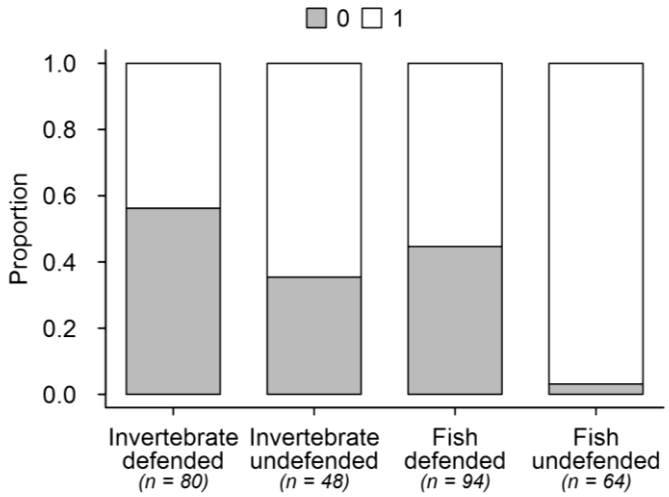


Figure 2. Proportion of experimental trials in which no prey were eaten (grey shading) or at least one of the prey was eaten (white shading) for different predator-prey groupings; predatory invertebrates-defended prey, predatory invertebrates-undefended prey, predatory fish-defended prey, predatory fish-undefended prey. Sample size (n) for each group indicated in brackets.

Per capita interaction strengths across all taxa

The data from the predator-prey combinations where at least one prey individual was eaten showed that the relationships between PPMR and per capita interaction strength was a limit response rather than a central tendency response. A significant positive linear limit relationship between $\log_{10}$ PPMR and $\log_{10}$ per capita interaction strength at the 95^{th} quantile was described using quantile regression analysis (slope = 0.41 ± 95% confidence interval (0.31-0.46), t = 7.78, $p<0.001$, Figure 3 a).

Linear models using $\log_{10}$ PPMR, the presence/absence of prey defences, year and associated interactions were used as predictors to further investigate relationships in per capita interaction strengths underneath the limit response described above. The interaction between log10 PPMR and prey defence and associated main effects, as well as the significant main effect of year, were included in the most parsimonious model, based on p-values (α=0.05) and type III sums of squares (Table 1). The significant interaction between $\log_{10}$ PPMR and prey defence was driven by there being no relationship between $\log_{10}$ PPMR and per capita interaction strength when prey were morphologically defended (Figure 3 b), and a positive relationship between $\log_{10}$ PPMR and per capita interaction strength when prey were

undefended (slope = 0.42 ± 0.04, Figure 3 c). The 'year' main effect was caused by slightly higher interaction strengths in 2011 compared to 2012 (Figure S 1). These higher interaction strengths could have been due to lower prey densities, different predators or prey, or a combination of all of the above.

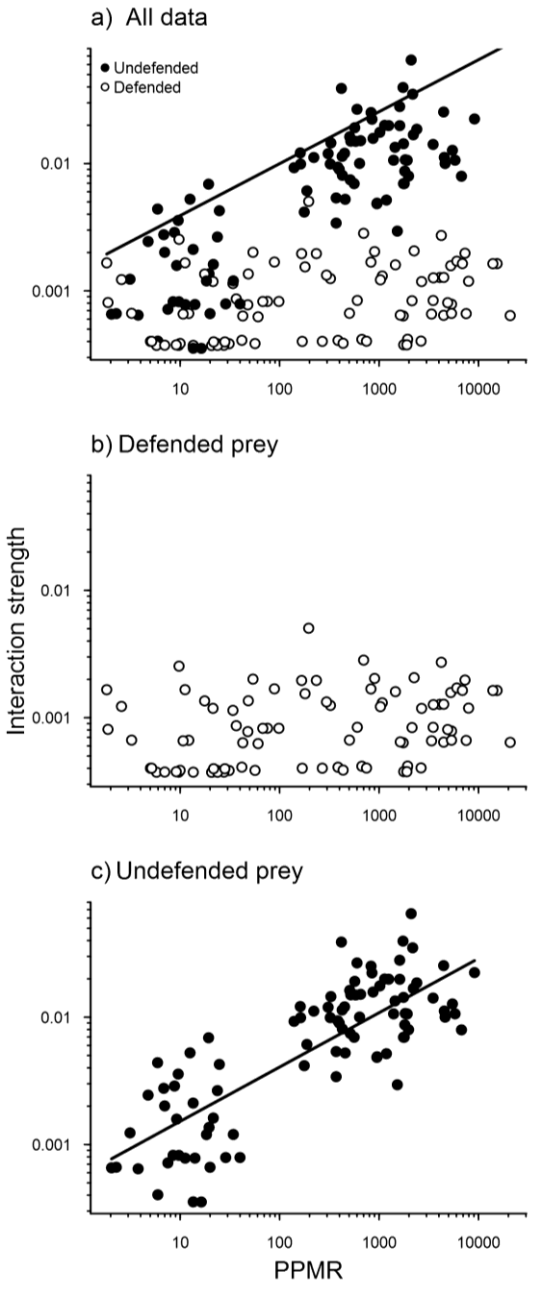


Figure 3. Relationships between predator prey mass ratio (PPMR) and per capita interaction strength, measured using the dynamic index for all prey (a), defended prey only (b), and undefended prey (c). Significant regressions are shown as a solid line. For combined defended and undefended prey (179 predator-prey pairs), the predicted regression line for the 95^{th} quantile is shown (a). Defended (b) and undefended (c) prey were combined in one analysis, and the significant regression lines were derived from the significant $\log_{10}$ PPMR prey defence interaction coefficient adjusted for the mean of the year effect.

Per capita interaction strengths – comparison of predatory invertebrates and fish

The same linear modelling analysis was used to investigate the relationships between $\log_{10}$ PPMR, prey defences and per capita interaction strengths in the predatory invertebrates and fish separately (Figure 4, Table 1). Predatory invertebrates and fish were split into two separate analyses because they occurred on different parts of the PPMR scale; predatory invertebrates were smaller and represented smaller PPMRs compared to the larger predatory fish (Figure 4). When the data were split into predatory invertebrates and fish, there was no significant effect of $\log_{10}$ PPMR on interaction strength (Figure 4, Table 1). However, there were significant main effects of both prey defence and year on interaction strengths (Figure 4, Table 1). Both predatory invertebrates and fish ate more undefended prey than defended prey across all PPMRs, and the effect of year (Table 1) was again driven by higher interaction strengths in 2011 compared to 2012 (Figure S 1).

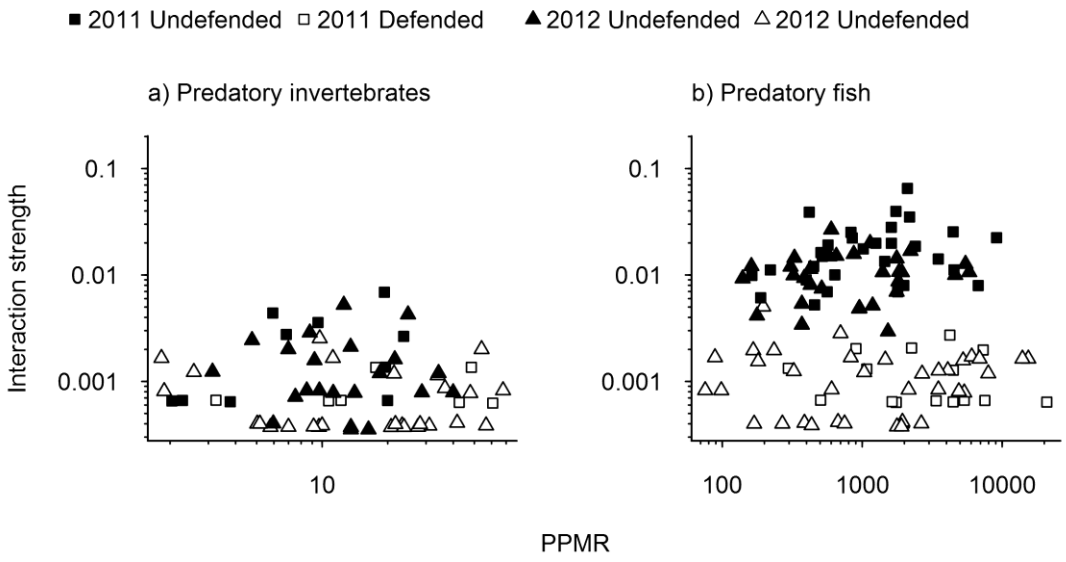


Figure 4. Relationships between predator-prey mass ratio (PPMR), and per-capita interaction strength (measured as the dynamic index) for predatory invertebrates (a) and predatory fish (b). Symbols indicate defended and undefended prey and the year, and are explained in the legend.

Table 1. Results based on linear models to explain per capita interaction strengths (number of prey eaten per hour) in the full data set (all data), for predatory invertebrates and for predatory fish.

	d.f.	SS	F	P
All data				
Log_{10} PPMR	1	10.14	119.33	<0.001
Prey defence	1	29.26	344.20	<0.001
Year	1	0.76	8.93	0.003
PPMR*defence	1	6.73	79.12	<0.001
Residual	174	14.80		
Model R^2= 0.77				
Predatory invertebrates				
Log_{10} PPMR	1	0.01	0.14	0.708
Prey defence	1	1.40	15.24	<0.001
Year	1	0.26	2.79	0.100
Residual	62	0.124		
Model R^2= 0.25				
Predatory fish				
Log_{10} PPMR	1	0.04	0.54	0.465
Prey defence	1	29.44	418.20	<0.001
Year	1	0.44	6.28	0.014
Residual	109	7.67		
Model R^2= 0.82				

Interestingly, out of all the individual predator and prey combinations included in this experiment, only the pairing between *G. vulgaris* and *Nesameletus* produced a significant positive relationship between PPMR and per capita interaction strength (Figure S 2). All other individual predator-prey pairings did not have a significant relationship between PPMR and interaction strength.

Mass specific interaction strengths

In comparison to per-capita interaction strengths, mass-specific interaction strengths had a negative relationship with increasing predator size for both defended (slope=-0.92) and undefended prey (slope=-0.61) (Figure 5). There was also a significant interaction between predator size and prey defences (p_{perm}<0.001, Figure S 3). However, the relationship between predator size and interaction strength for defended prey was no different than expected by random (Figure 5). In comparison, the negative relationship between predator size and mass-specific interaction strength was less negative than expected by random for undefended prey (Figure 5), thereby driving the interaction between predator size and prey defence.

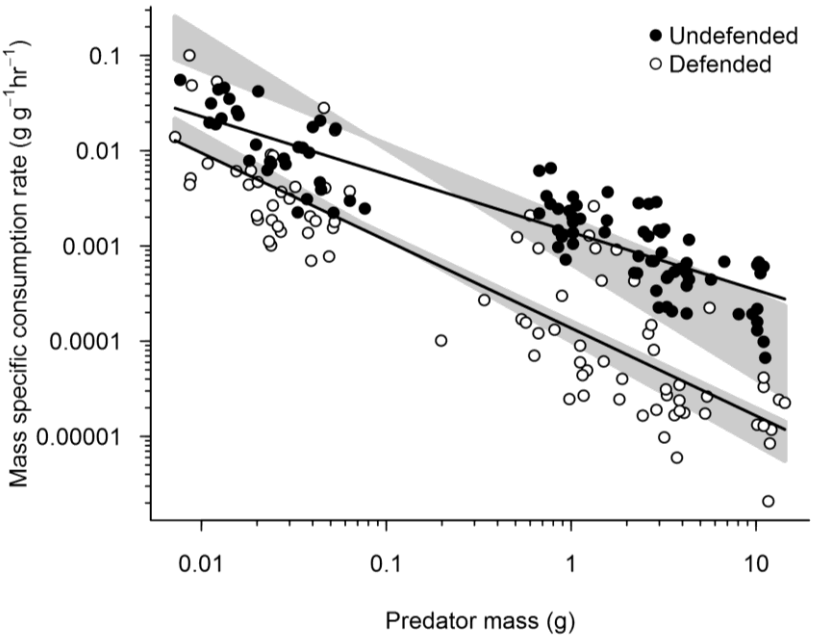


Figure 5. Relationship between mass specific interaction strength (biomass of prey eaten/predator mass/hour) and predatory mass (g). Grey shaded polygons represent the slopes that could be expected by random, generated from shuffling the y-axis numerator 9999 times in permutation tests to produce a 95% confidence interval. Regression lines are plotted based on the original linear model analysis.

Discussion

The relative distribution of weak and strong predator-prey interactions in ecological communities is an important determinant of food web stability (de Ruiter et al. 1995, McCann et al. 1998), and body size is thought to be a controller of the strength of predatory interactions within food webs, and therefore a useful proxy variable (Emmerson and Raffaelli 2004, Woodward and Warren 2007, Brose et al. 2008). My results indicate that, similar to previous studies, there is a positive relationship between predator-prey mass ratios (PPMRs) and per capita interaction strengths. However, unlike other studies, I have shown PPMRs were related to the maximum upper limit of per capita interaction strengths and variation in interaction strengths under this limit were largely explained by prey morphological defences. Moreover, across the range of predator-prey combinations used in this experiment the relationship between PPMR and interaction strength is significantly shallower than 0.75, indicating that theories including processes and traits over and above metabolism need to be developed to accurately estimate interaction strengths in food webs.

I created a gradient in PPMRs, predominately by manipulating predator size. Larger predators have higher overall metabolic demands and, therefore, higher energetic demands to satisfy (Peters 1983). Consequently, larger predators generally have greater potential to eat more prey compared to smaller predators in a set amount of time, driving the positive scaling of interaction strengths with PPMRs. Importantly, I have shown that this greater potential maximum per capita interaction strength associated with larger predators also leads to greater potential for variation in interaction strengths. Studies to date have reported central-tendency responses between predator body size and interaction strength and not limit responses (e.g. Emmerson and Raffaelli 2004, Klecka and Boukal 2013). Thus, by working in a different

system (streams) and examining the effects of prey traits (defence) I have demonstrated that interaction strengths can actually be quite variable.

For strong interaction strengths to occur across a gradient of PPMR, likely a number of conditions need to be met. For example, predators must be ideally matched to their prey (predator foraging traits match prey vulnerability traits perfectly), prey density needs to be high enough that a predator can encounter enough prey to reach satiation, and habitat structure needs to allow detection of prey (Boukal 2014). Therefore, the central tendency responses reported by other studies are likely to reflect ideal matching of predators with prey in conditions with limited refugia, allowing maximum interaction strengths to be realised. For example, in this study, the relationship between interaction strength and PPMRs for undefended prey showed a central-limit response similar to previous studies, albeit shallower, indicating that PPMRs would likely be a good predictor of interaction strengths when prey are palatable. However, in complex natural communities with many species and heterogeneous habitats it is likely factors other than body size, mean conditions allowing extremely high potential interaction strengths are not realised (Rossberg et al. 2010, Vucic-Pestic et al. 2010, Klecka and Boukal 2013). For example, I have shown that, interactions involving defended prey showed no relationship between interaction strength and PPMR. Thus, the predictive capacity of the relationship between interaction strength and PPMRs should be improved by inclusion of other easy-to-measure environmental variables and traits, of predators and prey, such as morphological defences, driving variation in interaction strengths.

In natural communities, the defended prey used in these experiments are all found in the diets of predators; some are probably associated with uncommon links and weaker food-web interactions, but others are commonly eaten, form major dietary components and are very

common food web links (Devonport and Winterbourn 1976, McIntosh 2000). Therefore, the frequency of non-feeding and the absence of very strong interactions with predators was not a result of testing for interactions that would not be found in nature. Both predator hunger and prey density also play important roles in the strength of predatory interactions (Holling 1959, Hileman et al. 1995), so it is possible running experiments longer or increasing density of defended prey resulting in increased encounter rates, may have increased interaction strengths. Nevertheless, my results suggest positive relationships between PPMR and interaction strengths involving defended prey in nature are only likely to occur at high prey densities or in situations where there are limited other prey options available.

Traits associated with predators may also account for differences in interaction strengths between this study and those undertaken previously. In this study, predatory invertebrates were more likely to have eaten no prey in an experimental trial compared to predatory fish, especially if the prey were defended. Additionally, in the treatments where at least one prey individual was consumed, predatory invertebrates ate fewer undefended prey than predatory fish, resulting in weaker per capita interaction strengths. These patterns likely reflect differences in PPMRs associated with each predator type. PPMR ranges found in nature typically increase with increasing predator size (Brose et al. 2006a, Barnes et al. 2010, Riede et al. 2011), and the average body mass ratios of predatory invertebrates are generally smaller than those of other predators (Brose et al. 2006a). This is similar to the patterns of PPMRs created in this study, where predatory invertebrates represented smaller PPMRs and fish larger PPMRs. Smaller PPMRs often lead to smaller per capita interaction strengths, probably because at smaller PPMRs predators are closer in size to their prey, and therefore require less prey to meet their energetic requirements (Brose et al. 2008). However, although smaller PPMRs lead to weaker per-capita interactions they are also associated with stronger *per biomass* effects (Werner 1994, Brose et al. 2006b, Klecka and Boukal 2013). I also found

this; predatory invertebrates in my study had higher mass specific interaction strengths compared to predatory fish. Consequently, although predatory invertebrates may have weaker per-capita interaction strengths in food webs, they are generally more numerous and have higher-mass specific interactions, and therefore at a population level may actually be stronger interactors than predatory fish.

Notwithstanding the differences in interaction strengths between predatory invertebrates and fish, the relationship between per capita interaction strength and PPMRs still broke down when either only predatory invertebrates or only fish were included in the analyses. For a positive relationship between per capita interaction strength and PPMR to occur using the dynamic index, large predators have to be able to eat a significantly greater proportion of prey than smaller predators. This occurred when both predatory invertebrates and fish were included in one analysis because there was a large range in PPMRs leading to large differences in the proportion of prey eaten by fish compared to invertebrates. However, "small" fish and "large" fish were able to eat similar proportions of prey, for example causing the relationship between PPMR and interaction strength to break down. This is potentially due to predators in this experiment being limited by prey density. Prey densities were within the range of prey densities of each prey found in the natural environment, but predators are typically presented with many different types of prey in natural habitats, so total prey densities would be higher than those used. Higher prey densities, that did not limit prey consumption of large predators, may have resulted in positive scaling relationships between PPMRs and per capita interaction strengths. Additionally, prey limitation may also explain the relatively shallow slopes of the overall relationship between interaction strengths and PPMRs (0.42 ± 0.04) found in this study compared to other studies (e.g. 0.54 and 0.66 from Emmerson and Raffaelli, 2004). This indicates that prey density could also be an important determinant of the relationship between PPMRs and per-capita interaction strengths.

Overall, abundant prey in addition to well-matched traits of predators and prey, are likely to allow relatively strong relationships between PPMRs and interaction strengths. For example, in this study the well matched combination of predatory *G. vulgaris* and *N. ornatus* mayflies had a relatively strong positive relationship between per capita interaction strength and PPMR. However, the combination of *G. vulgaris* and *N. ornatus* mayflies was the only individual predator-prey pairing to show this relationship. Therefore, the results of this study and knowledge of the wide variation in density as well as other traits such as, foraging mode and behaviour, seen in natural communities, indicates that the relationship between interaction strengths and PPMRs appear not to be as general as the literature might suggest.

In general, predator-prey interactions between well-matched predators and undefended palatable prey are likely to set the upper limit to interaction strengths, while further traits such as prey morphology likely explain the gradient of strong to weak interactions beneath this limit. Consequently, estimating interaction strengths based solely on PPMRs will likely overestimate the number of strong interactions in food webs and underestimate the number of weak interactions. Therefore, theory and subsequent models could be advanced by incorporating other easy-to-measure traits, in addition to body size, to improve the estimation of interaction strengths in ecological communities and to ultimately enable a better understanding of community dynamics.

Supplementary material

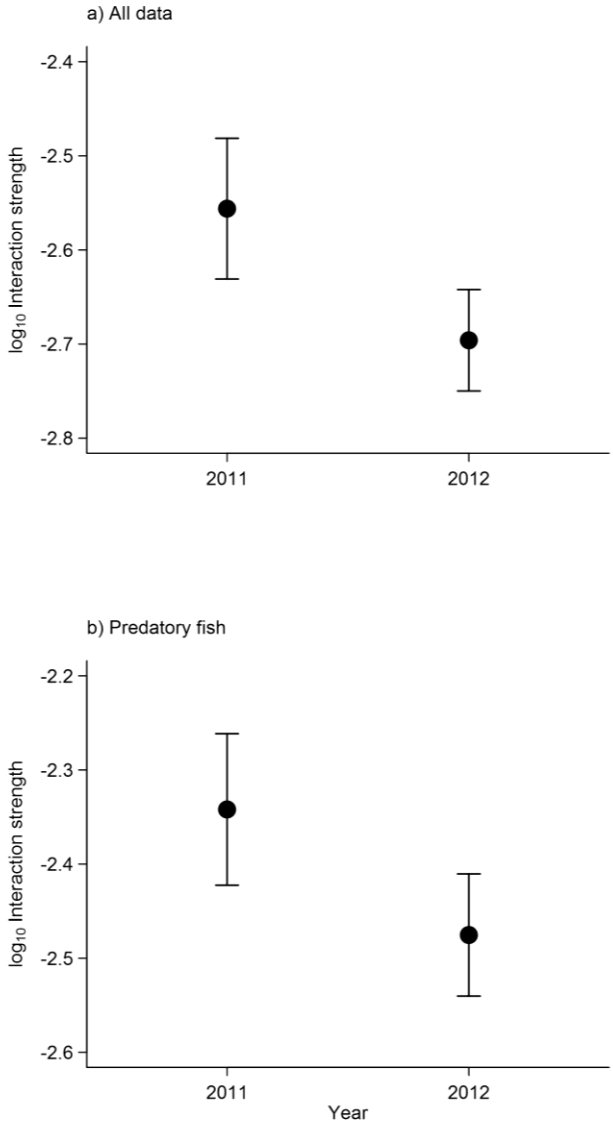


Figure S 1. Per capita interaction strengths (measured using the dynamic index) in each year. Values are fitted means based on linear models controlling for the effects of $\log_{10}$ predator prey mass ratio and prey defences. Error bars represent 95% confidence intervals.

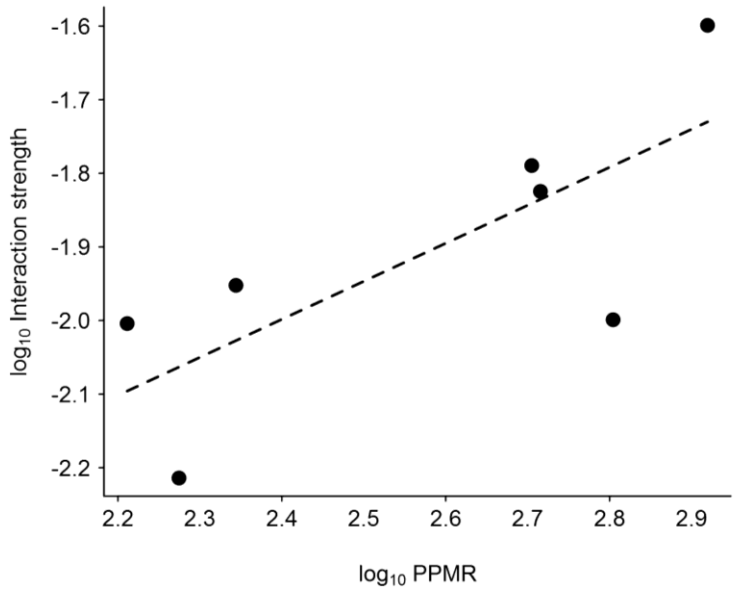


Figure S 2. Relationship between $\log_{10}$ predator prey mass ratio (PPMR) and $\log_{10}$ per capita interaction strength (measured using the dynamic index) for the predatory fish *Galaxias vulgaris* and the undefended mayfly prey *Nesameletus* (slope=0.52, p=0.05, R^2=0.56)

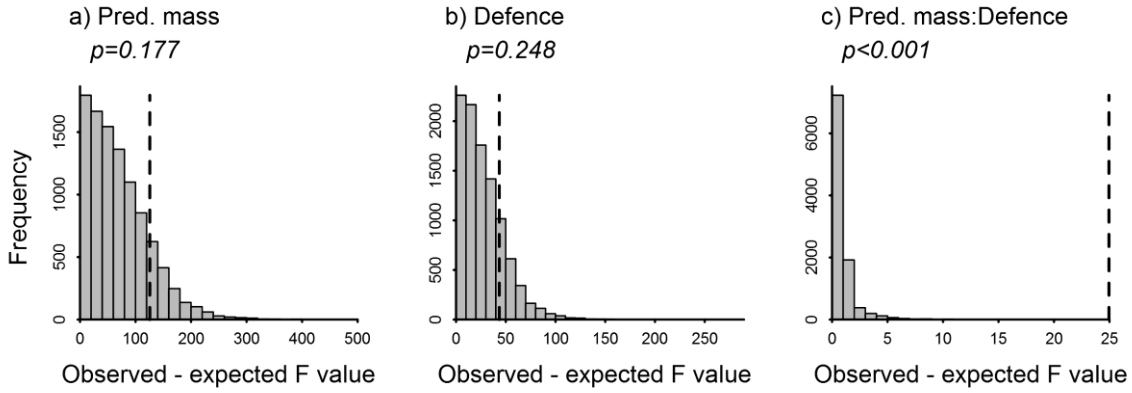


Figure S 3. Frequency histograms showing absolute values of observed (F-value from the original model) minus expected F-value (average of F-values based on a randomised numerator in permutation tests) for the effects of predator mass (grams) (a) and presence or absence of morphological prey defences (b), and the interaction between predator mass and prey defences (c) in the original linear model for mass-specific interaction strength. Dashed vertical lines represent observed F-values and P-values were determined from 9999 permutations.

Table S 1. Predator and prey combinations used in interaction strength experimental rounds in 2011 and 2012. Predator and prey species, number of times a predator prey combination was used in each year, and presence of prey defences are indicated. Numbers in brackets are the number of treatment combinations in which at least one prey individual was eaten. Predatory invertebrate species *Archichauliodes diversus* and *Stenoperla prasina* have been abbreviated to *Archi.* and *Steno. r*espectively.

		Prey	**Predatory invert.**		**Predatory fish**		
			Archi.	*Steno.*	*G.vulgaris*	*S. trutta*	***Total***
2011	**Defended**	*Coloburiscus*	-	-	-	-	-
		Olinga	8 (3)	-	8 (2)	8 (5)	*24 (10)*
		Potamopyrgus	8 (4)	-	8 (7)	8 (1)	*24 (12)*
		Pycnocentrodes	-	-	-	-	-
	Total (Defended)		*16 (7)*	-	*16 (9)*	*16 (6)*	*48 (22)*
	Undefended	*Deleatidium*	8 (7)	-	8 (8)	8 (8)	*24 (23)*
		Nesameletus	8 (3)	-	8 (7)	8 (8)	*24 (18)*
	Total (Undefended)		*16 (10)*	-	*16 (15)*	*16 (16)*	*48 (41)*
Total (2011)			*32 (17)*	-	*32 (24)*	*32 (22)*	*96 (63)*
2012	**Defended**	*Coloburiscus*	8 (-)	8 (7)	8 (7)	8 (5)	*32 (19)*
		Olinga	8 (5)	8 (4)	8 (5)	8 (2)	*32 (16)*
		Potamopyrgus	8 (1)	8 (2)	8 (5)	8 (3)	*32 (11)*
		Pycnocentrodes	8 (7)	8 (2)	7 (5)	7 (5)	*30 (19)*
	Total (defended)		*32 (13)*	*32 (15)*	*31 (22)*	*31 (15)*	*126 (65)*
	Undefended	*Deleatidium*	8 (7)	8 (6)	8 (8)	8 (8)	*32 (29)*
		Nesameletus	8 (5)	8 (3)	8 (7)	8 (8)	*32 (23)*
	Total (undefended)		*16 (12)*	*16 (9)*	*16 (15)*	*16 (16)*	*64 (52)*
Total (2012)			*48 (25)*	*48 (24)*	*47 (37)*	*47 (31)*	*190 (117)*
Total			*80 (42)*	*48 (24)*	*79 (61)*	*79 (53)*	*286 (180)*

Table S 2. Size range of predators (a) and mean size of prey ± standard error (b), used in the experiment and the source of the length-weight regression equations used to convert length into dry mass.

Species	Predator size range/prey size (g)	L-W source
a) Predators		
Archichauliodes diversus	0.0035-0.063	Towers et al. (1994)
Galaxias vulgaris	0.20-8.05	Jellyman et al. (2013a)
Salmo trutta	0.67-14.31	Jellyman et al. (2013a)
Stenoperla prasina	0.0086-0.077	Towers et al. (1994)
b) Prey		
Coloburiscus humeralis	6.46 (± 0.19)	Towers et al. (1994)
Deleatidium sp.	1.80 (± 0.06)	Towers et al. (1994)
Nesameletus ornatus	4.64 (± 0.16)	Towers et al. (1994)
Olinga sp.	2.31 (± 0.05)	Towers et al. (1994)
Potamopyrgus antipodarum	0.58 (± 0.01)	Baumgärtner and Rothhaupt (2003)
Pycnocentrodes sp.	0.88 (± 0.01)	Towers et al. (1994)

Table S 3. Densities of prey species found in a wide range of streams in the Cass region based on data from Chapter Two, converted to equivalent numbers per tank (tank area, 0.21 m^2). Mean density and range (minimum and maximum) of densities found in streams are shown.

Species	Mean number	Range
Coloburiscus humeralis	24	1-72
Deleatidium sp.	276	28-945
Nesameletus ornatus	6	1-13
Olinga sp.	26	1-68
Potamopyrgus antipodarum	118	1-600
Pycnocentrodes sp.	41	1-411

Table S 4. Results from a binomial generalised linear model to determine if there was a significant effect of predator type (invertebrate, fish) and prey type (defended, undefended) on the proportion of trials where no prey were eaten.

	Residual d.f.	**Residual deviance**	**P**
Null	3	58.02	
Predator	2	45.14	<0.001
Prey defence	1	10.96	<0.001
Predator*defence	0	0	<0.001

Chapter Four

Scaling relationships between predator size, prey size and interaction strength depend on prey abundance

Introduction

The interconnected nature of organisms within a community makes them susceptible to perturbations because changes to individual species abundance can propagate throughout the community, influencing many other species and even connected communities (Dunne et al. 2002, Montoya et al. 2009). Food webs are important descriptors of these aspects of ecological communities, describing connections between predators and prey, predominantly via feeding interactions (Cohen et al. 1993, Dunne 2009). Because not all links in food webs are of equal strength, the structure of unweighted links alone is unlikely to be effective in predicting the effects of species perturbations on food-web stability and function (Paine 1988, Polis 1991, Tylianakis et al. 2007, Novak et al. 2011). However, the relative distribution of weak and strong links (weighted links) in food webs, measured through interaction strengths (the magnitude of the effect of one species on another), is an important driver of food-web stability (McCann et al. 1998, McCann 2000, Neutel et al. 2002), influencing how communities respond to environmental stress and biotic perturbations (e.g. species invasions). Therefore, for understanding and predicting how communities will respond to future environmental stress and perturbations, parameterising food webs with accurate estimates of interaction strengths is critical.

Estimating the strength of all feeding interactions within a community, let alone across different communities, is logistically challenging (Morales-Castilla et al. 2015). Therefore,

more easily measured proxy variables are needed to estimate interaction strengths within and across multiple communities (Morales-Castilla et al. 2015). Body size has potential to be such a proxy. It has long been recognized that predators are generally larger than their prey (e.g. Elton 1927), and many communities, especially aquatic communities, appear to be highly size-structured (Cohen et al. 2003, Woodward et al. 2005, Petchey et al. 2008). Moreover, body size is relatively easy to measure and plays an important mechanistic role in many aspects of feeding ecology (Woodward and Warren 2007, Brose et al. 2008). This has motivated the development of relationships between body size and interaction strengths that can be used to parameterise food-web models (Jonsson and Ebenman 1998, Emmerson et al. 2005).

The link between body size and metabolism through a positive power-law relationship with a scaling exponent of 0.75 (Peters 1983, Brown et al. 2004), is one of the main mechanistic links between body size and interaction strengths (Emmerson et al. 2005, Schmitz and Price 2011). For example, as predator size increases, metabolic demand increases and therefore, consumption rates should also increase to match increased energetic demands. In addition to predator size, the strength of interactions between predators and prey within food webs should also depend on the size of prey being consumed; a predator will require more small compared to large prey to meet their energetic demands (Brose et al. 2008). Consequently, the size ratio between predators and prey should be an important determinant of interaction strengths in food webs (Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Emmerson et al. 2005, Brose et al. 2008).

Recently, predator-prey mass ratios (PPMRs) have been shown to scale positively with interaction strengths using the dynamic index (equivalent to the Lotka-Volterra interaction coefficient) in a marine estuary ecosystem (Emmerson and Raffaelli 2004), and further

theoretical studies indicate the scaling coefficient of the relationship between interaction strength and PPMR should be 0.75, based on well-established allometric relationships (Emmerson et al. 2005). However, limited empirical tests of this relationship across different ecosystem types exist.

As much as body size should be an important driver of interaction strengths in food webs, other traits of predators and prey are also likely to be important in explaining interaction strength patterns. Predator foraging mode and prey vulnerability (Klecka and Boukal 2013, Chapter Three), and the abundance of predators and prey (Holling 1959, Barbosa et al. 2005) are also likely to affect the strength of interactions, potentially altering the relationship between PPMRs and interaction strengths. Prey abundance, for example, influences predator consumption rates, as illustrated by functional responses which describe how consumption rates change with changing prey abundance (Holling 1959).

Although functional responses, which measure consumption rates, measure interaction strengths differently than the dynamic index (Berlow et al. 2004) used by Emmerson and Raffaelli (2004), they reveal how prey abundance influences the relationship between PPMR and interaction strength. Specifically, they show that predators only reach maximum consumption rates at high prey densities, when they are not limited by prey detection, encounter or attack rates (Jeschke et al. 2002, Brose et al. 2008). Maximum consumption rates are the ones hypothesized to be controlled by metabolic demands (Brose et al. 2008), therefore, the predicted allometric scaling relationship between PPMR and interaction strength (exponent 0.75, Emmerson et al. 2005) may only hold at high prey densities, when predators can actually reach their maximum consumption rates. At lower prey densities, scaling relationships between PPMR and interaction strength are likely to be shallower because large predators, relative to their prey, are limited by prey availability and will not

reach their maximum consumption rates. Therefore, at low prey densities, interaction strengths are likely to be more similar between small and large PPMRs than would be predicted based on current theory.

The densities of organisms in food webs varies greatly, both temporally and spatially, being affected by many factors. Additionally, many species in food webs are rare, and by definition have low abundance (Magurran and Henderson 2003). Therefore, understanding how the relationship between PPMR and interaction strengths varies across density gradients is important for improving the accuracy of body-size based estimates of food-web interaction strength. Here I ran a mesocosm experiment to specifically test if interaction strength scaled with PPMR using undefended palatable prey and a range of invertebrate and vertebrate predators from both pond and stream habitats. I also tested if the relationship between PPMR and interaction strength increased with increasing prey density, and tested if the slope of the relationship between PPMR and interaction strength depended on the measure of interaction strength used (dynamic index or consumption rate).

Methods

To test whether the relationship between interaction strength and predator-prey mass ratio (PPMR) was dependant on prey density I used six different prey densities (5, 50, 70, 100, 150, 200 per tank), two predator-prey pairings from ponds and five predator-prey pairings from stream habitats (Table S 1). For each predator species used a gradient of predator size was created by using five individuals that ranged from small to large (Table S 2). This resulted in 210 individual predator-prey feeding trials (7 combinations x 5 predator sizes x 6 densities).

Mesocosms

The mesocosms (circular basins, 52 cm wide), were used to replicate either stream (flowing) or pond (still) environments (Figure 1), and were filled with filtered water pumped from an adjacent perennially-flowing stream which drains a lake. For stream trials, water flow (0.04 ± 0.0005 $m.s^{-1}$) in mesocosms was created by two water jets facing in opposite directions on each side of a central standpipe (3 cm wide; Figure 1); water flowed around each mesocosm and then drained back out into the stream. For pond trials, flow was minimised by reducing water pressure from the jets and facing the jets upright to stop water flow around the tanks. A mesh-covered standpipe maintained water depth (12.5 cm), the base of each mesocosm was painted with non-toxic pond paint mixed with sand to create a rough surface suitable for aquatic invertebrates to walk on, and terracotta saucers and pots were used to create fish and invertebrate cover in each mesocosm (Figure 1). The terracotta saucers and pots were colonised with algae prior to each trial to provide food for invertebrates, and after each trial the substrates were exchanged with freshly colonised saucers and pots. Mesocosms were also covered with mesh lids to prevent fish escaping. A maximum of 36 mesocosms were used in any experimental round and light conditions were standardised in each round using a 12 hour light-dark period.

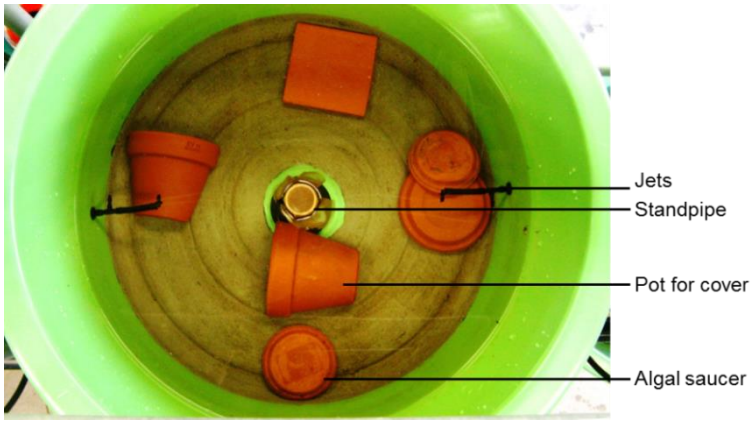


Figure 1. Mesocosm set-up, with terracotta pots and saucers for fish cover and algal growth surfaces, jets generating circular flow around the tank (52 cm wide), and the stand pipe (3 cm wide) maintaining water depth (12.5cm).

Experimental design

Predator species were selected to represent a natural size gradient and included both predatory invertebrates and fish. To create a gradient of predator size, five individuals of each species that ranged from small to large were used once in each experimental round (Table S 2). Two predator species *Gobiomorphus breviceps* (upland bully) and *Procordulia grayi* (dragonfly) were sourced from local ponds and were paired with locally abundant chironomid larvae (*Chironomus* sp.) as prey (Table S 1). *Salmo trutta* (brown trout) and *Stenoperla prasina* (stonefly) from stream habitats were paired with *Deleatidium* sp. and *Nesameletus* sp. mayfly nymphs as well as *Chironomus* sp. larvae as prey (Table S 1). Prey taxa were specifically chosen to be undefended, palatable prey, to maximise the strength of feeding interactions with predators, and to ensure the tightest possible relationship between predator prey mass ratio (PPMR) and interaction strength. Prey sizes (Table S 2) were selected to be as uniform as possible within each prey species, and animals were sourced from local streams and rocky lake shores using a combination of electrofishing/bugging, sweep netting, Gee minnow trapping and cobble-sampling techniques.

Predators were collected the day prior to an experimental round and acclimated, one per mesocosm, overnight prior to prey being added. A total of 36 trials (a single meocosm containing a single predator-prey pairing) could be run in any one experimental round (one 24 hour experiment period, a maximum of 36 mesocosms),. Therefore, the seven possible predator-prey pairings were randomly assigned to separate experimental rounds, but all prey density and predator size combinations for the selected predator-prey pairings were run in the same experimental round. After prey were added to tanks, predators and prey were left in mesocosms for approximately 24 hours, after which predators were removed, and remaining prey were counted. In each experimental round at least one control trial (i.e. with no predator)

for each prey taxon and density being used was left for the same period, and used to adjust for counting errors and to calculate prey dry weights. Invertebrate predator and prey lengths were measured post-experiment from preserved animals, whereas fish lengths were measured prior. The dry weights of predators and prey were calculated from length-weight regressions (Table S 2) and used to calculate biomass.

Statistical analysis

Per capita interaction strengths were calculated using the dynamic index, also known as the log-ratio method (Berlow et al. 1999, Berlow et al. 2004):

$$Interaction\ strength_{(dynamic\ index)} = \frac{\log\left(\frac{P}{C}\right)}{Xt} \qquad \text{(Equation 1)}$$

Where *P* was abundance of prey in the presence of predators, *C* was abundance of prey in the absence of predators which was calculated using all the control trials at the appropriate density for each prey species. *X* was abundance of predators, and *t* was the time period over which the experiment was run (hours).

Analysis of covariance (ANCOVA) was used to test if the relationship between PPMR and interaction strength changed with prey density. All predator-prey pairs were used in the one analysis and treated as replicates of PPMR, therefore testing the universality of the relationship between PPMR and interaction strength at the community level. Density was included in the analysis as a categorical factor and PPMR as a continuous variable. The absolute value of the interaction strength was used in all analyses; stronger interactions indicated by larger positive numbers. Both PPMR and interaction strength were $\log_{10}$-transformed to improve homogeneity of variances. Treatments in which all prey were eaten (this occurred in four of the five *G. breviceps*-*Chironomus* treatments) and treatments in

which no prey were eaten (Table S 3) were removed from analyses due to constraints of the logarithm transformation and artifacts in results created by adding constants to zero values. The removal of treatment combinations resulted in an unbalanced design, so analyses were based on type III sums of squares where the significance of each term was only tested when it was added in the model last.

I used the regression equations between $\log_{10}$ PPMR and $\log_{10}$ interaction strength for each prey density to determine if changes in interaction strengths at the smallest or largest end of the PPMR gradient caused the slope of the relationship between PPMR and interaction strength to change with prey density. To calculate the predicted interaction strength for the smallest or largest PPMR, I substituted in the smallest and largest PPMR, respectively, into the regression equation and calculated the predicted interaction strength for each density. Additionally, I ran all of the above analyses using consumption rate (number of prey eaten per hour) as a different commonly used measure of interaction strength which is also used in functional response experiments to determine how dependent the slopes of the relationship between PPMR and interaction strength were on the interaction strength metric chosen. All analyses were carried out in R 3.1.2 (R Core Team 2015).

Results

I ran a total of 210 different predator-prey combinations, using four different predator species, three different prey species and six different prey densities. I used 183 of these combinations in the analyses; 27 had to be removed due to either all prey, or no prey, being eaten. Analysis of these 183 predator-prey pairs revealed relatively consistent positive relationships between increasing PPMR and interaction strength measured using the dynamic

index (Figure 2). Moreover, a significant interaction between PPMR and prey density in ANCOVA indicated the slope of the relationship between PPMR and interaction strength depended on prey density (Figure 2, Table S 4). Slopes of the relationship between PPMR and interaction strength ranged (dynamic interaction strength absolute value ± 95% confidence interval) from 0.1 ± 0.11 to 0.46 ± 0.15, and increased in the range of 5 and 40 prey per mesocosm, after which there was no change in slope (Figures 2 & 3a). These changes in slope with prey density were driven by a decrease in interaction strength for treatments with the smallest PPMRs because predators ate a smaller proportion of the available prey as density of prey increased (Figure 3c).

Similar relationships between PPMR and interaction strength were found across the different prey densities when using consumption rate as the measure of interaction strength instead of the dynamic index (Figure 3b, Figure S 1). The major difference between the two interaction strength indices was what drove the changes in slope. When prey density increased, the main driver of slope increase in the PPMR and consumption rate relationship was an increase in interaction strength for the largest PPMR, whereas for the dynamic index no differences in interaction strength at the largest PPMRs were found (Figure 3c &d).

The slopes of the relationship between PPMR and interaction strength (dynamic index) were highly variable for each of the individual predator-prey pairs in which all five predator-prey pairings were available. Slopes ranged from 0 to 1.48, with slopes from only 11 out of 29 predator-prey pairs being significantly different from zero in regression analysis.

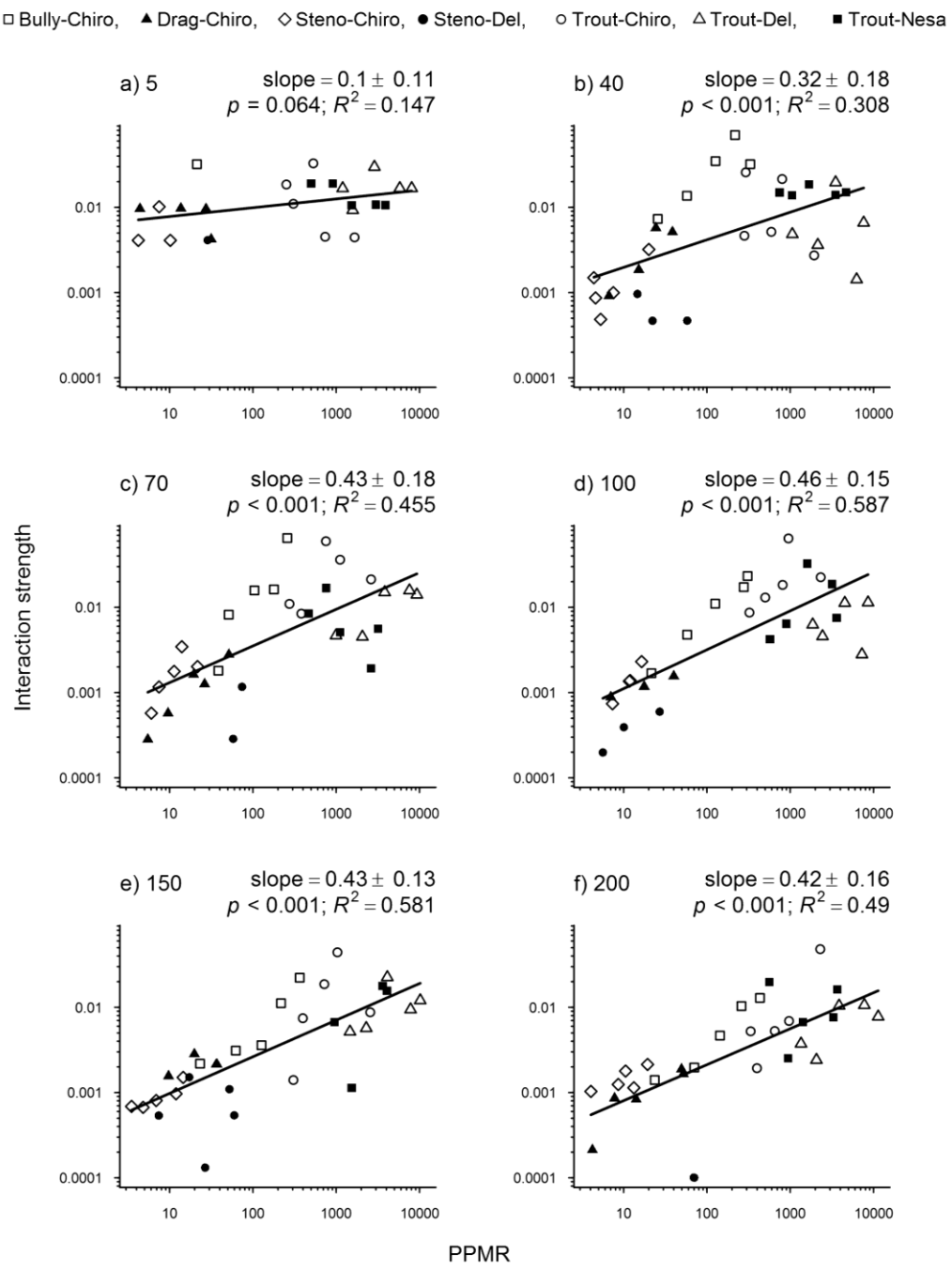


Figure 2. Relationships between predator-prey mass ratio (PPMR, dry weight of predator/dry weight of prey [g]) and interaction strength (dynamic index, absolute value) for different prey densities (numbers of prey per tank = 5, 40, 70, 100, 150, 200, a-f respectively) and with different predator-prey pairings indicated by different symbols. Regression lines and slopes (± 95% confidence intervals) are from linear regression models, and associated p-values and R^2 values are indicated on the plots. Predator-prey pairings are as follow, with symbols indicated above the plots: *Gobiomorphus breviceps* (upland bully) and *Chironomus*, Bully-Chiro; *Procordulia grayi* (dragonfly) and *Chironomus*, Drag-Chiro; *Stenoperla prasina* and *Chironomus*, Steno-Chiro; *Stenoperla prasina* and *Deleatidium*, Steno-Del; *Salmo trutta* (brown trout) and *Chironomus*, Trout-Chrio; *Salmo trutta* (brown trout) and *Deleatidium*, Trout-Del; *Salmo trutta* (brown trout) and *Nesameletus*, Trout-Nesa.

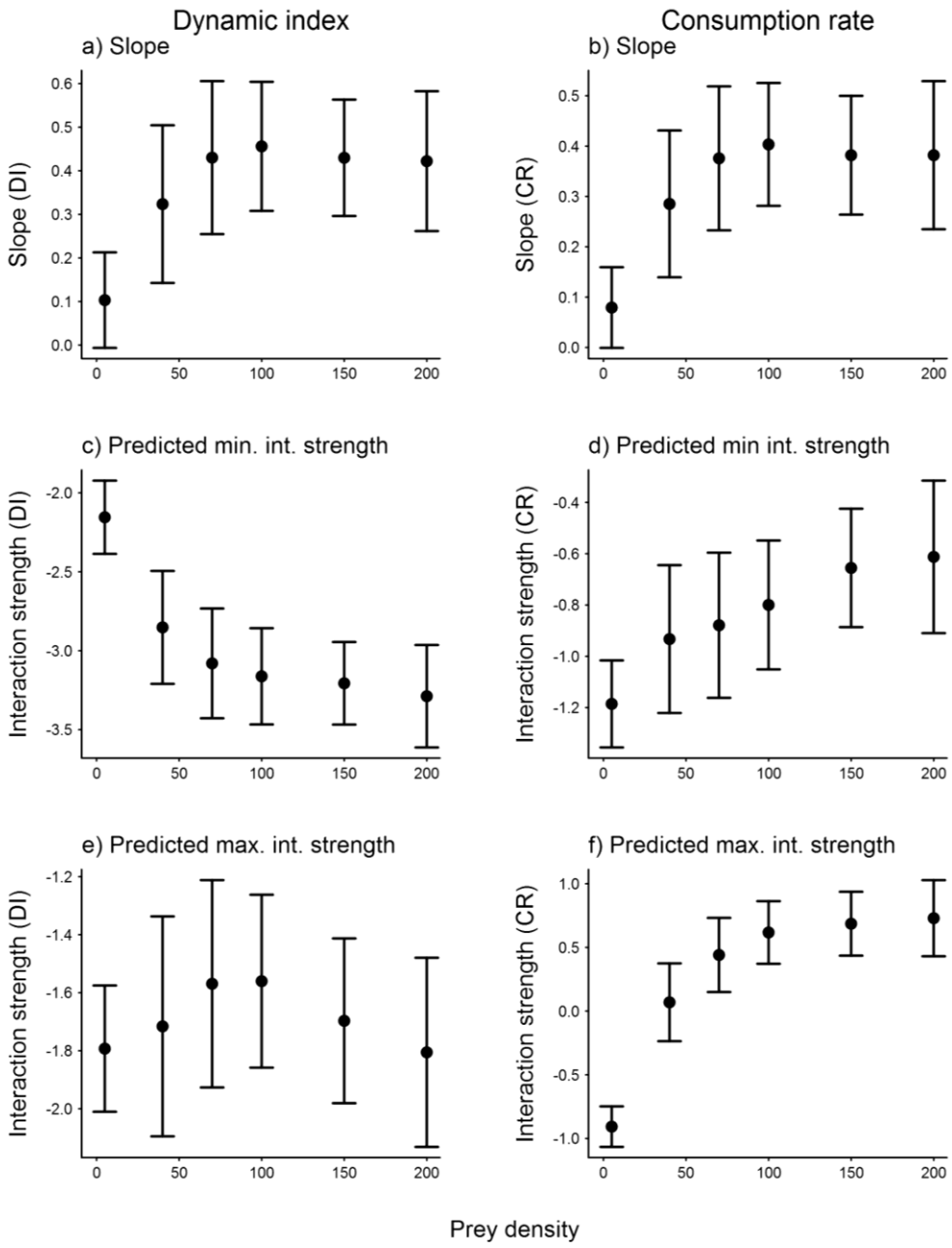


Figure 3. Plots showing changes in interaction strength related measures with prey density (number per mesocosm) and type of measure (dynamic index [DI] or consumption rate [CR]).The slope coefficients (a, b), predicted minimum interaction strengths (c, d) and the predicted maximum interaction strengths (e, f) are calculated from the relationships between predator-prey mass ratio (PPMR) and associated measures of predator impact on prey. Relationships between PPMR and interaction strength calculated using the dynamic index are shown in Figure 2 and consumption rate in Figure S 1. 95% confidence intervals are plotted.

This experiment was designed to test the relationship between PPMR and interaction strength across all the different predator-prey pairs, so there was no replication for each PPMR within each different species predator-prey pairing. Therefore, analyses at the individual level were highly influenced by a predator's interaction strengths at either end of the PPMR gradient. However, this analysis of individual predator-prey pairs highlighted that for some specific, well-matched, predator and prey pairings, a tight relationship between PPMR and interaction strength existed, and that the slope of the relationship could be steeper than the community-averaged relationship (Figure 4). For example, the slopes of the relationship between PPMR and interaction strength for the pairings of *P. grayi* and *Chironomus*, and for *G. breviceps* and *Chironomus* had slopes of 0.71 ± 0.58 and 0.83 ± 0.39, respectively.

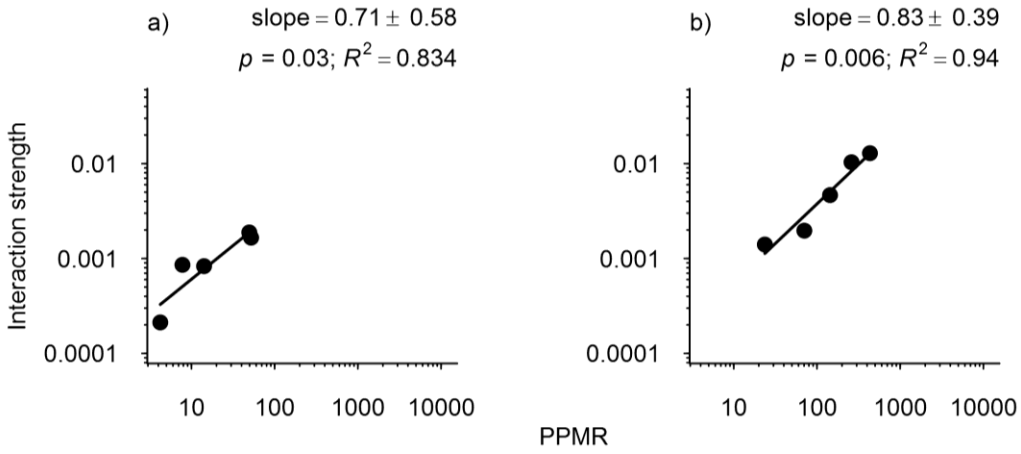


Figure 4. Regressions of predator-prey mass ratio (PPMR, dry weight of predator/dry weight of prey [g]) and interaction strength (dynamic index, absolute value) at the prey density of 200 per tank for the predator-prey pairings of the dragonfly, *Procodulia grayi* and *Chironomus* (a), and the fish, upland bully, *Gobiomorphus breviceps* and *Chironomus* (b). Regression lines and slopes (± 95% confidence intervals) are from linear regression models, and associated p-values and R^2 values are indicated on the plots.

Discussion

Predation is an important food-web interaction which determines the structure and dynamics of communities (Barbosa and Castellanos 2005) and body size is a key trait driving those predatory interactions (Woodward and Warren 2007). My study adds to a growing body of research on the size-structuring of communities and it provides empirical tests of controls on the relationship between predator prey mass ratios (PPMRs) and interaction strengths. As expected, similar to previous research (e.g. Emmerson and Raffaelli 2004), interaction strength increased with increasing PPMR in the majority of treatments, indicating that for vulnerable prey PPMRs are a reliable predictor of predator-prey interaction strengths. However, although interaction strengths were strongly related to PPMRs, the slope of the relationship varied significantly with changes in prey density, and this has important implications for what we understand the drivers of interaction strength to be, and how we subsequently use these interaction strength measures.

At low prey densities, consumption rates of prey by predators are restricted by prey detection, encounter and attack rates. In comparison, at high prey densities predators are not limited by prey availability, and consumption rates are constrained by handling times, which are inversely proportional to maximum consumption rates (Jeschke et al. 2002, Koen-Alonso 2007). Consequently, at low prey densities in this experiment, larger predators were likely not able to reach maximum consumption rates despite their potentially greater energetic demands, meaning that steeper slopes between PPMR and interaction strength could not occur. Therefore, the shallower slopes between PPMR and interaction strength I measured at low densities are most likely driven by larger predators being prey-limited. Thus, consideration of the interaction strength drivers in communities, over and above body size, shed further light on the PPMR-interaction strength relationship.

There are many different measures of interaction strength used in both empirical and theoretical studies (Berlow et al. 2004). Although the magnitude of interaction strengths calculated by both the dynamic index and consumption rate are not comparable, they both provide insight into how prey density affects the relationship between interaction strength and PPMR. Interaction strengths of larger predators relative to their prey, measured by consumption rates, increased with prey density. This was highlighted by an increase in the consumption rates for large PPMRs as prey density increased from 5-70 prey per tank. At higher prey densities, consumption rates of large predators were constant indicating that predators were no longer limited by prey availability.

Compared to consumption rates, the dynamic index measure is essentially a proportion of prey eaten, and at low prey densities, predators that were close in size to their prey (i.e. small PPMRs) were able to eat the same proportion of prey as predators that were large compared to their prey (i.e. large PPMRs). Therefore, when using the dynamic index, the steeper slopes observed at high prey densities, were driven by smaller predators eating a smaller proportion of the available prey. Consequently, as prey density increases, interaction strengths based on the dynamic index, as opposed to those based on consumption rates, weakened because smaller proportions of prey were eaten. Nevertheless, despite differences in the two interaction strength indices, they both revealed similar relationships between interaction strength, PPMR and prey density, therefore, both would estimate relatively the same distribution of weak and strong interactions across a PPMR gradient.

There was no difference in the slopes of the relationship between PPMR and interaction strengths in the four highest prey density treatments indicating that predators were not limited by prey availability in these treatments. Despite this, based on the dynamic index, the steepest slope between PPMR and interaction strengths (0.46 ± 0.15) was significantly shallower than

the slope of 0.75 predicted by allometric theory (Emmerson et al. 2005). Recent studies have also found shallower than predicted scaling relationships between predator size and interactions strengths (Chapter Three, Pawar et al. 2012, Rall et al. 2012, Kalinkat et al. 2013, Klecka and Boukal 2013) indicating that interaction strengths are not solely constrained by metabolic process. For example, organism traits, such as predator foraging mode, prey vulnerability, and habitat complexity and dimensionality could all influence the predation process over and above body size, resulting in shallower slopes than expected based on the relationships derived from metabolic theory (Pawar et al. 2012, Kalinkat et al. 2013).

Potentially both prey vulnerability and habitat structure, over and above body size and prey density, may have affected the strength of predator-prey interactions in my experiment. I specifically chose prey without morphological defences to include the strongest possible interactions between predators and prey based on previous research (Chapter Three). However, prey vulnerability can also be a product of a prey's ability to escape predatory encounters which would also modify the relationship between PPMR and interaction strength (Klecka and Boukal 2013, Chapter Three). In this experiment the steepest slopes between PPMR and interaction strengths, which were not significantly different to 0.75, were between predators and, the most vulnerable prey, chironomids. Although this experiment was not specifically designed to test the relationships between interaction strengths and the individual predator-prey pairs, these relationships provide some insight into potential factors beyond body size that influence interaction strengths.

Chironomids are much less mobile than the two mayfly species used as prey in other pairings, and are therefore potentially more vulnerable to predation. Moreover, compared to mayfly prey which could hide under the terracotta substrates, chironomid prey had potentially less suitable habitat refugia, therefore making them even more vulnerable. This suggests that both

prey mobility and habitat structure, which reduce prey vulnerability independent of body size, may lead to shallower slopes between PPMR and interaction strength than would be predicted by allometric theory.

Variations in the density, traits of predators and prey, and habitat structure of natural environments are common and are likely to influence the reliability of PPMRs for predicting predator-prey interaction strengths based on current theory. Allometric relationships probably do a good job of predicting the relationship between PPMRs and interaction strengths when prey are abundant and vulnerable to predators. However, rarely was the slope of the relationship between $\log_{10}$ PPMR and $\log_{10}$ interaction strength as steep as 0.75 in my experiment and importantly, the relationship between PPMR and interaction strength became much shallower at low prey densities. Therefore, my results indicate that the distribution of weak and strong interaction strengths in a food web, is likely to be quite different based on the relationships developed in this study, compared to those predicted by current metabolic based theory. This highlights the need for more empirical tests of allometric scaling relationships, and especially those based on the metabolic theory, across different communities, to identify key, measurable and generalisable traits and aspects of communities other than body size that can be used to inform and enhance allometric theory. My work indicates that understanding the effects of prey density and prey vulnerability will be an important addition to these relationships.

Supplementary material

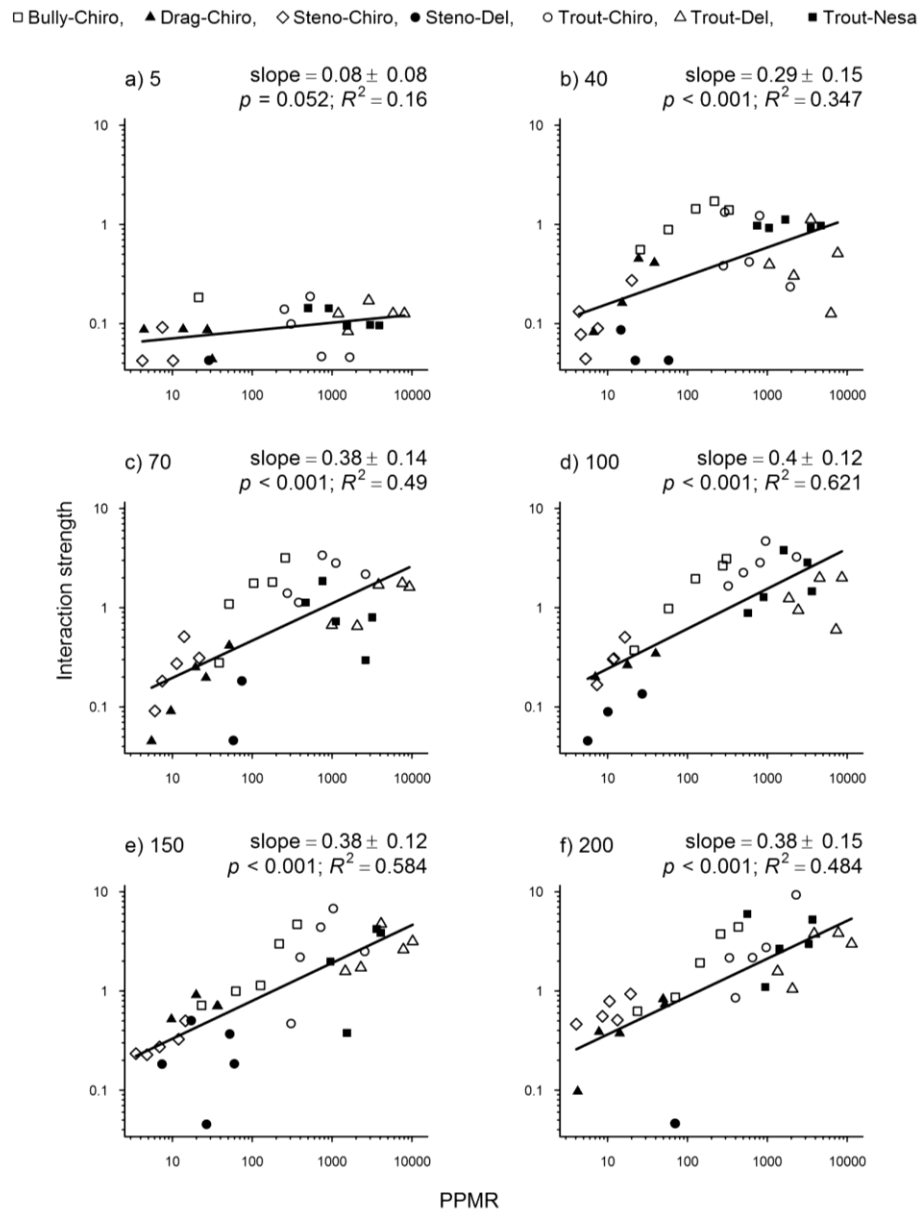


Figure S 1. Relationships between predator-prey mass ratio (PPMR, dry weight of predator/dry weight of prey [g]) and interaction strength (consumption rate, number of prey eaten per hour) for different prey densities (numbers of prey per tank = 5, 40, 70, 100, 150, 200, a-f respectively) and with different predator-prey pairings indicated by different symbols. Regression lines and slopes (± 95% confidence intervals) are from linear regression models, and associated p-values and R^2 values are indicated on the plots. Predator-prey pairings are as follow, with symbols indicated above the plots: *Gobiomorphus breviceps* (upland bully) and *Chironomus*, Bully-Chiro; *Procordulia grayi* (dragonfly) and *Chironomus*, Drag-Chiro; *Stenoperla prasina* and *Chironomus*, Steno-Chiro; *Stenoperla prasina* and *Deleatidium*, Steno-Del; *Salmo trutta* (brown trout) and *Chironomus*, Trout-Chrio; *Salmo trutta* (brown trout) and *Deleatidium*, Trout-Del; *Salmo trutta* (brown trout) and *Nesameletus*, Trout-Nesa.

Table S 1. Predator and prey pairings used in the experiments. Habitat indicates whether the mesocosms were run as stream or pond mesocosms.

Predator	Predator type	Prey	Habitat
Gobiomorphus breviceps	Fish	*Chironomus* sp.	Pond
Procordulia grayi	Invertebrate	*Chironomus* sp.	Pond
Salmo trutta	Fish	*Chironomus* sp.	Stream
Salmo trutta	Fish	*Deleatidium* sp.	Stream
Salmo trutta	Fish	*Nesameletus ornatus*	Stream
Stenoperla prasina	Invertebrate	*Chironomus* sp.	Stream
Stenoperla prasina	Invertebrate	*Deleatidium* sp.	Stream

Table S 2. Size range of predators (a) and mean size of prey (± standard error) (b), used in the experiment and the source of the length-weight regression equations used to convert length into dry mass.

Predator	Predator size range/prey size (g)	L-W source
a) Predators		
Gobiomorphus breviceps	0.07-1.36	Jellyman et al. (2013a)
Procordulia grayi	0.01-0.16	Stoffels et al. (2003)
Salmo trutta	0.78-12.34	Jellyman et al. (2013a)
Stenoperla prasina	0.005-0.07	Towers et al. (1994)
b) Prey		
Chironomus sp.	3.42 (± 0.05)	Stoffels et al. (2003)
Deleatidium sp.	1.12 (± 0.02)	Towers et al. (1994)
Nesameletus ornatus	2.75 (± 0.05)	Towers et al. (1994)

Table S 3. Predator -prey combinations and density treatments in which no prey were eaten. The number of trials column indicates how many of the size classes within a particular combination did not have any prey eaten.

Predator	Prey	Density	Number of trials
Procordulia grayi	*Chironomus* sp.	5	1
Stenoperla prasina	*Chironomus* sp.	5	2
Stenoperla prasina	*Deleatidium* sp.	5	4
Procordulia grayi	*Chironomus* sp.	40	1
Stenoperla prasina	*Deleatidium* sp.	40	2
Stenoperla prasina	*Deleatidium* sp.	70	3
Procordulia grayi	*Chironomus* sp.	100	2
Stenoperla prasina	*Chironomus* sp.	100	1
Stenoperla prasina	*Deleatidium* sp.	100	2
Procordulia grayi	*Chironomus* sp.	150	1
Salmo trutta	*Nesameletus ornatus*	150	1
Stenoperla prasina	*Deleatidium* sp.	200	3

Table S 4 Results from analysis of covariance (ANCOVA) using log_{10}PPMR as a continuous predictor, prey density as a categorical predictor and log_{10} absolute value of the dynamic interaction strength as the response.

	d.f.	SS	F	P
Log_{10} PPMR	1	25.90	5.99	<0.001
Prey density	5	4.82	5.19	<0.001
PPMR*density	5	2.54	2.74	0.02
Residual	171	31.77		
Model R^2 = 0.52				

Chapter Five

Biomass-independent, top-down effects of predator body size and abundance on lower trophic levels

Introduction

The body size of organisms in a community is likely to play an important role in the structure and stability of food webs (Cohen et al. 2003, Woodward et al. 2005, Petchey et al. 2008, Kalinkat et al. 2013). For example, organism body size typically increases with trophic level, decreases with abundance, and per capita feeding interactions often increase with organism body size (Emmerson and Raffaelli 2004, Jennings 2005, Woodward et al. 2005, White et al. 2007, Brose et al. 2008). Therefore, large top predators in food webs are generally rare, but are likely to interact strongly with other species, potentially controlling the abundance and dynamics of lower trophic levels (Fretwell 1987, Dobson et al. 2006, Estes et al. 2011). Consequently, the loss of top predator biomass can restructure communities, alter food-web dynamics and cause trophic cascades, making top predators particularly important for community stability, function and provision of ecosystem services (Duffy 2003, McCann et al. 2005, Dobson et al. 2006, Schmitz et al. 2010, Estes et al. 2011). Large top predators, because of their size and low abundance, may be particularly vulnerable to anthropogenic changes, such as habitat loss and overfishing (Pauly et al. 1998, Duffy 2003, Dobson et al. 2006). Consequently, it is important to understand how changing top predator size-structure and biomass influences food web structure and dynamics.

Summary data are often used when evaluating top predator biomass in food webs, for example, the total or average biomass of all individuals of a particular species in a

community is commonly used as a node in food-web analysis (Woodward et al. 2010, Gilljam et al. 2011). However, different sized individuals of the same species may have different metabolic rates, diets, and behaviour (e.g. Woodward and Hildrew 2002, Brown et al. 2004, Hansen and Closs 2005, Rudolf and Rasmussen 2012). Therefore, using species summary data can mask potentially important differences in feeding interactions of different sized individuals within the same species (Ings et al. 2009, Rudolf et al. 2014).

Body size is closely related to metabolism; since metabolism scales with body mass to the power 0.75 (Peters 1983, Brown et al. 2004). This relationship underpins an organism's energetic demands and ultimately is thought to drive the strength of feeding interactions within food webs (Emmerson and Raffaelli 2004, Brose et al. 2006a, Kalinkat et al. 2013). Therefore, among predators, larger predators should have greater per capita energetic demands than smaller predators and therefore stronger per capita feeding interactions (Emmerson et al. 2005, Schmitz and Price 2011). However, population-level effects of predators on lower trophic levels are a product of both the abundance of a predator species and the per-capita feeding interactions attributed to those predators, which will be influenced by their body size (Figure 1). Therefore, if per-capita feeding interactions scale with predator metabolic rate and body mass ($M^{0.75}$), then population-level interactions should scale with population metabolic biomass (abundance [N] $\times$ body mass $[M]^{0.75}$) rather than directly to biomass ($N \times M^{1.0}$) (Schmitz and Price 2011). Accordingly, total predator biomass comprised of larger proportions of small predators should have a larger population-level effect on a community because the collective mass of smaller predators would have a greater total metabolic demand (Schmitz and Price 2011, Schneider et al. 2012). These population-level predator effects on lower trophic levels will likely include both direct consumption depressing prey biomass (Figure 1) and potentially also indirect effects on primary producers resulting from trophic cascades (Paine 1980, Power 1990). Thus, knowledge of how top

predator biomass is divided between small and large predators in a food web is important for understanding the impacts that top predators will likely have on lower trophic levels.

In addition to body size, predator density can affect the strength of predatory interactions in food webs through changes in competitive interactions among predators, such as mutual interference (Culp 1986, Kratina et al. 2009, Lang et al. 2012, DeLong and Vasseur 2013). Intermediate levels of competitive interactions are thought to stabilise communities because they weaken potentially strong predator-prey interactions, since the time spent by predators interacting with conspecifics reduces time spent feeding (Arditi et al. 2004, Kratina et al. 2009, Lang et al. 2012). However, elevated levels of predator interference at high predator densities can push populations towards extinction (DeLong and Vasseur 2013). Interestingly, mutual interference can be broadly independent of predator body size (DeLong 2014). Therefore although allometic theory might predict that top predator biomass consisting of smaller individuals will have stronger population interactions compared to equivalent total biomass consisting of a few large individuals, this effect might be dampened at high densities due to increased competitive interactions among the small predators.

To investigate how the division of top predator biomass between large and small predators influenced community structure at lower trophic levels, I ran an in-stream channel experiment in which I manipulated the size and abundance composition of top predatory fish while holding the overall top predator biomass constant. The experiment was designed to balance top predator biomass whilst also subdividing that biomass between different numbers (abundance) of predators ranging in body size (i.e., 1 large fish, 2 medium fish…down to 13 small fish) to test the biomass-independent top-down influences of predator abundance and body size on biomass at lower trophic levels. I predicted that despite having the same top predator biomass, channels in which that biomass was divided between a higher abundance of

smaller top predators, compared to channels with larger top predators, would have a larger influence on lower trophic levels, reducing the biomass of primary consumers and increasing algal biomass signalling strengthened top-down effects.

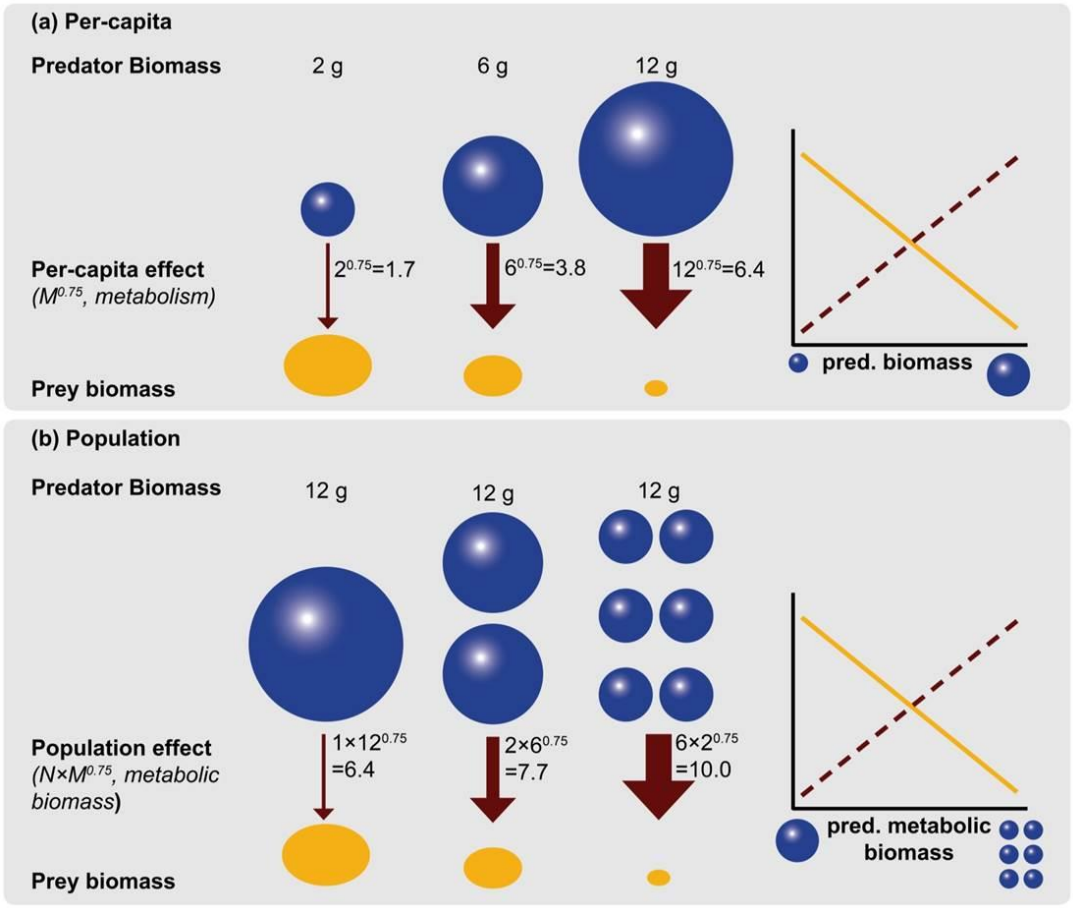


Figure 1. Conceptual diagram illustrating the per-capita (a) and population-level (b) consumptive effects of changing top predator size on prey at lower trophic levels. Blue spheres indicate predators, yellow ovals indicate prey biomass and dark red arrows indicate the top down-effect of predators on prey. Graphs to the right on each panel show the top-down predator effect (dark red dotted line) and the associated change in prey biomass (yellow line) with either increasing per-capita predator biomass (a) or increasing predator metabolic biomass for the whole predator population (b). Per-capita top-down effects (a), based on metabolic theory, should be related to a predator's metabolic rate which should scale with mass$^{0.75}$. Therefore, as predator size increases (increasing sphere size), the per capita top-down effect of predators should also increase (increasing arrow thickness in cartoon, and positive slope in graph). An increase in top down consumptive effects means that prey biomass left in the system should decrease with increasing predator size (decreasing yellow ovals, negative slope in yellow line on graph). Population-level top-down effects (b), should be related to predator population metabolic rate (predator abundance [N] × predator mass$^{0.75}$). Therefore, for a given top predator biomass, more small predators will have a greater top down effect and consequently depress prey biomass more than fewer larger predators. Per-capita and population top down effects are equivalent to grams of prey eaten.

Methods

The experiment was carried out using in-stream channels from the 14 February to 20 March 2013 in Grasmere stream, Cass, South Island, New Zealand. Grasmere Stream is a stable lake-fed stream flowing through tussock grassland with a fish fauna comprising of brown trout (*Salmo trutta*), Chinook salmon (*Oncorhynchus tshawytscha*) and longfin eels (*Anguilla dieffenbachii*) a diverse benthic invertebrate fauna and high water quality (Death and Winterbourn 1995, Nyström and McIntosh 2003).

Channels

Channels were constructed with a wooden frame, bottom and sides made of flexible PVC plastic sheeting, wire mesh ends, and fabric mesh on the tops (Figure 2). They were 1.8 m long and 0.45 m in diameter, creating 0.81 m^2 surface area. The mesh channel ends had 6.5-mm openings, allowing free immigration and emigration of invertebrates but preventing fish entering or escaping.

Each channel was filled with a layer of cobbles sourced from a dry river bed. Four baskets (0.038 m^2) filled with gravel and smaller cobbles were placed along the length of each channel were used for sampling invertebrate communities (Figure 2). Nine terracotta substrates (9 cm diameter) used for sampling algal biomass were placed in three rows of three between each basket in the channel. Channels were placed in the stream in pairs (each pair >20 m apart, Figure 2) for 26 days prior to adding fish to allow colonisation of invertebrate and algal communities. Channels were fully submerged so that the base of the channel sat flush with the stream bed and were cleaned at least every two days to prevent blocking.

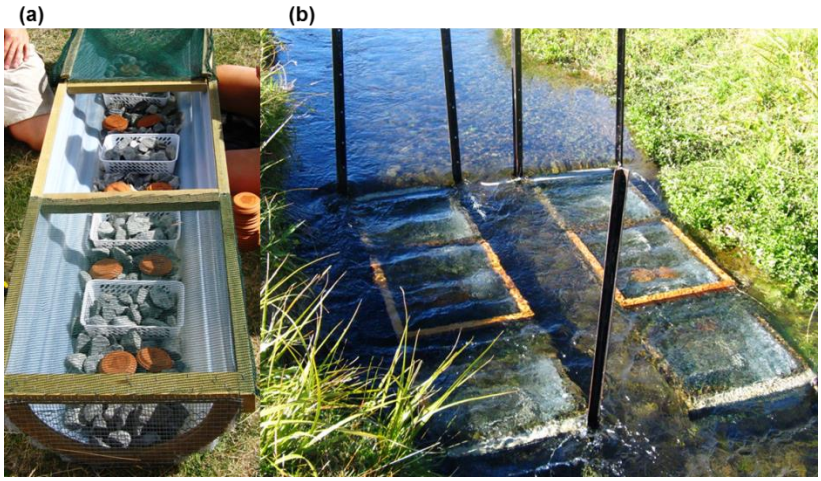


Figure 2. Stream channel (a) constructed from a wooden frame, PVC flexible plastic sides and base, wire mesh ends (6.5 mm openings) and mesh cloth lids and a pair of channels (b) placed on the bottom of Grasmere stream. Each channel was 1.8 m long and 0.45 m wide. The photo on the left shows an early set up inside the channel, but the final design had three rows of three terracotta saucers (9 cm in diameter) for sampling algal biomass, placed in between four baskets (15.7 cm x 23.9 cm) used for sampling invertebrates. Pairs of channels were placed at least 20 m apart.

Experimental design

To test how the division of top predator biomass among different body sizes affected top-down influences on the community, I manipulated the size and abundance of brown trout (*Salmo trutta*) added to each channel, creating five different fish abundance/size treatments. An abundance gradient was established with either one, two, four, seven or thirteen fish per channel. In addition, I also specifically manipulated fish size to try and match total fish biomass in each treatment. Thus a gradient from one large fish to thirteen small fish per channel was created. My aim was to match dry weight biomass of predatory fish across treatments; biomass of both invertebrates and algae were also calculated as dry weight. Each of the five treatments and controls were replicated four times using a randomised complete block design to account for possible longitudinal variation in community composition and environmental conditions along the stream.

The fish were collected from local streams using electrofishing and they, along with two large cobbles for extra fish cover, were added to the channels on 12 March 2013. The experiment ran for nine days before being disassembled because there was evidence that fish condition, especially in high density treatments, was starting to deteriorate. At the end of the experiment, fish were weighed then euthanized, and invertebrates from each basket were stored in ethanol and the terracotta algal tiles were frozen. To calculate the biomass of fish in each channel, a wet weight to dry weight conversion established from fish collected previously from the Cass region was used. Invertebrates were sieved with a 500-μm sieve, identified and the length every individual found in the front basket of each channel was measured using image analysis. Established length-weight regressions were used to convert invertebrate lengths to weights in dry mass (Towers et al. 1994, Stoffels et al. 2003). Algal biomass was measured using the front three algal substrates in each channel. After thawing, the biofilm on the top of each substrate was gently removed with a toothbrush, filtered onto a glass fiber filter (Whatman GF/C), dried for at least 24 hours at 50 ^{o}C and then ashed for four hours at 550 ^{o}C. Algal biomass was calculated using the ash free dry mass (AFDM) method described in Biggs and Kilroy (2000).

Analysis

Due to our inability to balance brown trout length and dry weight exactly when setting up the experiment, fish biomass was not the same across all treatments; instead there was a significant positive relationship between fish numbers and biomass driven by the smallest and largest fish size treatments (Figure 3, Table S 1). To evaluate effects of top predator number and biomass on primary consumer and algal biomass, the main response variables, a model selection approach using Akaike's Information Criterion corrected for small sample size

(AICc) (Burnham and Anderson 2002) was used to determine the weight of evidence in support of fish biomass, fish abundance or a block only model.

Post-hoc regression analysis indicated that there was no relationship between fish biomass and abundance across treatments with two, four and seven fish (Figure 3, Table S 1). Analysis of variance (ANOVA), including a block term, was used to explicitly test the effect of fish size and numbers on prey biomass (all primary consumers), predatory invertebrate biomass, and the biomass of algae in these three treatments where dry weight fish biomass was balanced. Additionally, in these treatments I also calculated the ratio of predators (fish and predatory invertebrates combined) to prey, to get a coarse estimate for how the community biomass structure, analogous to a biomass pyramid, changed with varying fish size and abundance.

Finally, to determine the effects of increased density and biomass of predators on prey biomass and algal biomass using all treatments, linear regression including a block term for treatment block location, was used. In both these analyses and in the analysis between algal biomass in the subset of data where predatory fish biomass was balanced, the number of fish was $\log_{10}$ transformed to deal with non-linearity in the relationship. All analyses were carried out using R 3.1.2 (R Core Team 2015).

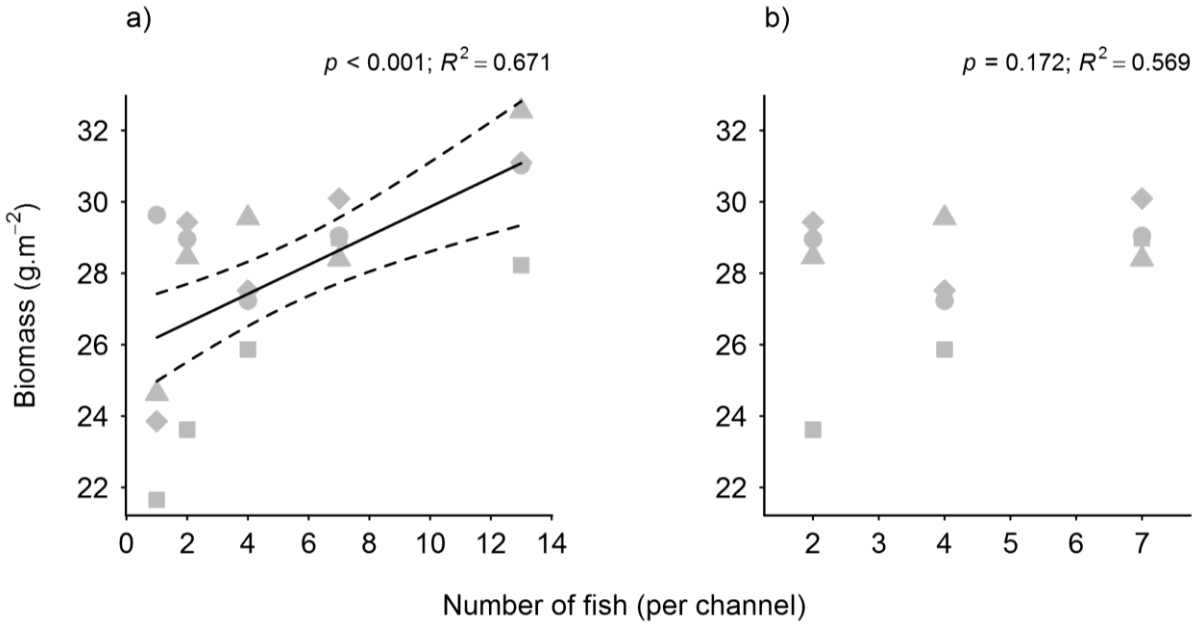


Figure 3. Relationship between the number of fish and total fish biomass (g dry weight.m^{-2}) in all treatments (a): 1, 2, 4, 7, 13 fish per channel, and in the treatments where biomass was balanced (b): 2, 4, 7 fish per channel. Symbols represent the four different blocks and R^2 and p-values associated with the fish biomass main effect and the full model including the block effect from analysis of variance are displayed.

Table 1. Model selection results for evaluating whether fish numbers, biomass or a block-only model were best for predicting prey biomass in the experimental channels. K is the number of parameters in the model, n is the number of data points, R^2 is the coefficient of determination, AICc is Akaike's Information Criterion with small sample size correction, Δi is the difference between the AICc of the given model and the model with the lowest AICc, ω_i is the Akaike weight and Evidence ratios were calculated using Akaike weights comparing subsequent models to the top model.

Model	**K**	**n**	**R^2**	**AIC_c**	**Δ_i**	**ω_i**	**Evid. ratio**
Prey biomass = Log_{10}(Abundance) + Block	6	20	0.55	68.60	0.00	0.72	1.00
Prey biomass = Block	5	20	0.36	71.54	2.93	0.17	4.33
Prey biomass = Log_{10}(Biomass) + Block	6	20	0.46	72.41	3.80	0.11	6.70

Results

Manipulating the size and abundance of the top predators, brown trout, resulted in significant changes to both invertebrate and algal biomass (Figure 4 & 5, Table 1 & S 2, S 3). My initial goal was to balance the total fish biomass by manipulating the size of individual fish across all of the five different abundance treatments (i.e. 1, 2, 4, 7, 13 fish per channel). However, since there was a significant positive relationship between fish dry weight and numbers (Figure 3, Table S 2), I could not test the independent effects of changing fish abundance and size on lower trophic levels using all treatments without the results also being confounded by increased biomass. Nevertheless, analysis of the full range of fish densities with model selection provided some useful insights. Both fish numbers and fish biomass had a significant negative relationship with prey biomass (Figure 5a, Figure S 1), but model selection indicated that a model with fish abundance and the block term as predictors was 6.7 times more likely to be the better predictor of prey biomass in the channels than a model with fish biomass and the block term (Table 1). Moreover, a model with just the block term was better than the model including fish biomass as the predictor (Table 1). Thus, analysis of all abundance treatments indicated that biomass was not as good a predictor of prey biomass in the channels as predator number.

Post-hoc analysis indicated that there was no relationship between fish biomass and abundance in the three treatments with two, four, and seven fish per channel (Figure 3, Table S 1). Therefore, changes in community responses across these treatments were a reflection of changes in top predator abundance/size but not biomass. In these treatments there was a significant negative relationship between prey biomass remaining in the channels at the end of the experiment and predator abundance (and a significant block effect; Figure 4a, Table S

2a). Prey biomass decreased from approximately three grams of dry mass per m^2 in channels with two fish to two grams of dry mass per m^2 in channels with seven fish.

Using this dataset with fish biomass balanced, there was no significant change in predatory invertebrate biomass across the predator abundance/size gradient (Figure 4b, Table S 2b). Decreases in prey biomass were also matched by increases in algal biomass across the increasing predator abundance/size gradient (Figure 4c, Table S 2c), reflecting a strengthening of top-down control. However, the relationship between increasing fish abundance and decreasing algal biomass was not linear since the number of fish was log transformed in analysis, indicating that the effects of increasing fish abundance might taper off. Additionally, the ratio of total predator biomass to total prey biomass had a significant positive relationship with increasing predator abundance/decreasing predator size (Figure 4d, Table S 2d), indicating increasingly top-heavy biomass pyramids.

Although fish biomass increased with increasing fish abundance when all five fish abundance treatments were included in analyses, it was useful to use the full dataset to test whether the significant effects of fish abundance on prey and algal biomass (negative and positive, respectively), seen in the balanced subset of data, were likely to continue in a linear fashion or taper off. Across all treatments, there was a significant negative relationship between $\log_{10}$ fish abundance and prey biomass and a significant positive relationship between $\log_{10}$fish abundance and algal biomass (Figure 5, Table S 3). These results indicate that at the very highest fish abundance and biomass tested, the effects of top predators on the rest of the community weakened, indicative of a tapering-off of interaction strength when fish abundance was very high.

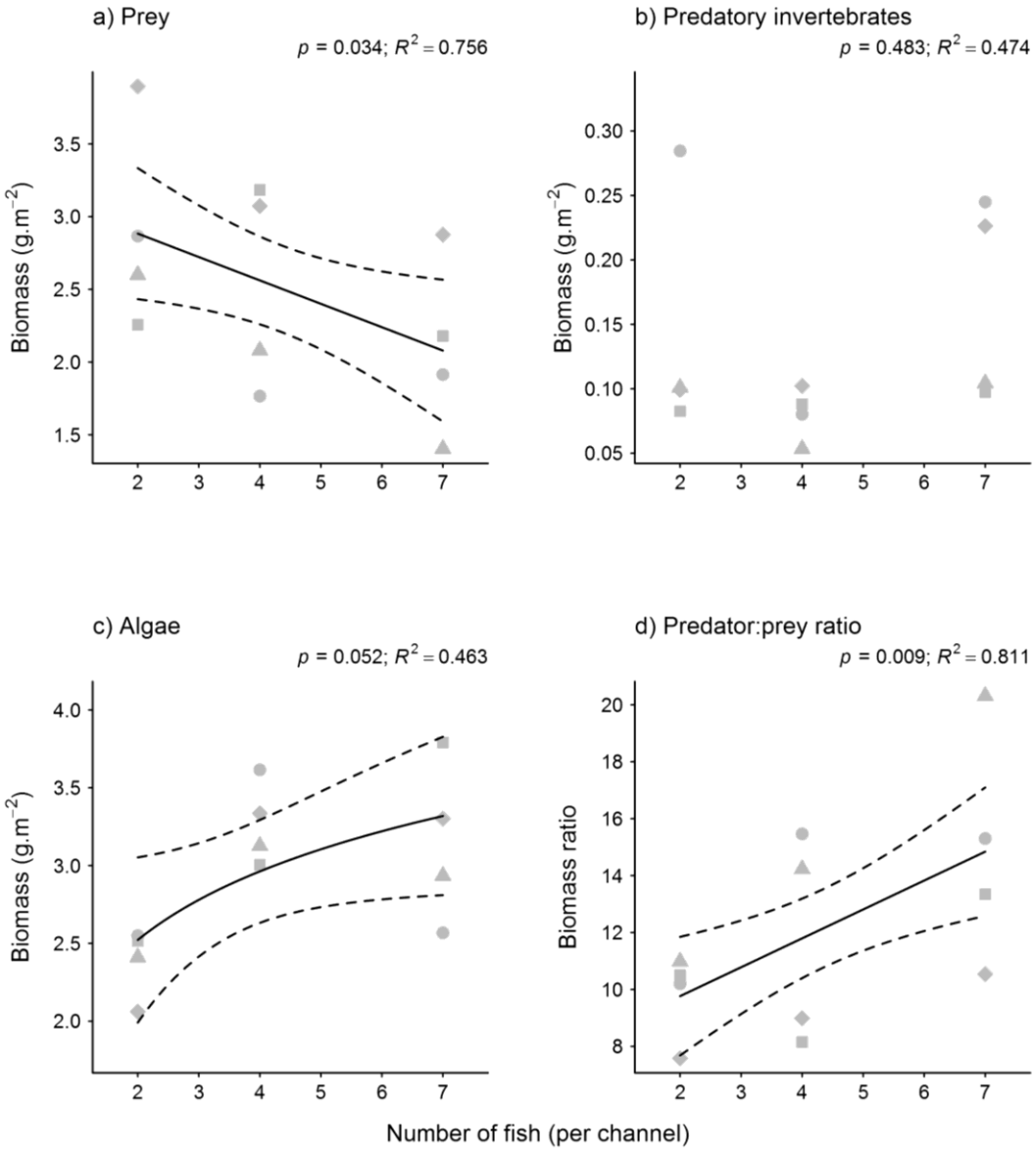


Figure 4. Relationship between the number of fish and prey biomass (a), predatory invertebrate biomass (b), algal biomass (c), and predator:prey biomass ratio (d). Biomass was measured in grams of dry weight per m^2. Different symbols represent the four different blocks. Significant regression lines and 95% confidence intervals were fit from the number of fish main effect accounting for any block effect. The p-value associated with the number of fish main effect and the R^2 for the full model including the block effect are displayed. The number of fish axis was $\log_{10}$ transformed for the analysis of algal biomass and the regression line and axis have been back-transformed for plotting.

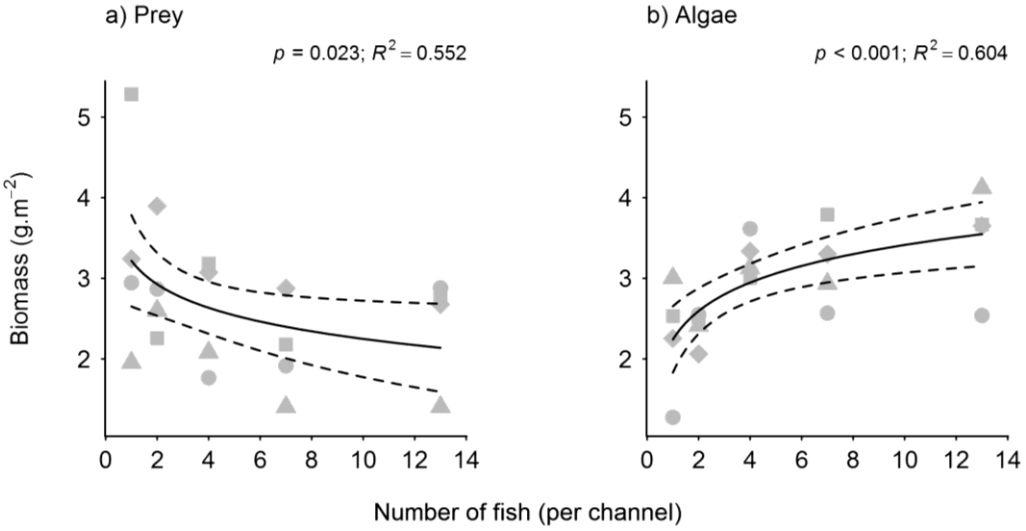


Figure 5. Relationships between number of fish and prey biomass (a), and predatory invertebrate biomass (b), using all fish abundance/size treatments. Biomass was measured in grams of dry weight per m^2. The different symbols represent the four different blocks. Significant regression lines and 95% confidence intervals were fit from the number of fish main effect accounting for any block effect. The p-value associated with the number of fish main effect and the R^2 for the full model including the block effect are displayed. The number of fish axis was log-transformed for the analysis, and the regression line and axis have been back transformed for plotting.

Discussion

In this study I have shown that considering how top predator biomass was subdivided between small and large individuals, not just the total amount of top predator biomass, was important for understanding the influences that top predators had on lower trophic levels. When biomass matching was not achieved, top predator biomass alone was not the best predictor of changes in prey biomass, indicating that the abundance and size of predators, over and above total predator biomass, were important drivers of community change. Moreover, dividing total top predator biomass between many small predators, compared to few large predators, had greater cascading impacts on the rest of the community. Therefore, the results of this experiment provide evidence supporting predictions from allometric theory, suggesting that more small predators should have a greater impact on lower trophic levels because of greater per-biomass energetic demands which combine to produce greater total population metabolic demands, summarised as a greater metabolic biomass (Schmitz and Price 2011, Schneider et al. 2012).

In this experiment, it was hypothesised that more small predators, compared to fewer large predators, would have a greater impact on lower trophic levels based on theory related to energy requirements (*sensu*, Schmitz and Price 2011). However, in natural communities, predators can potentially influence the dynamics of lower trophic levels through numerous different direct and indirect mechanisms, including both density-and trait-mediated interactions (Peacor and Werner 1997, Lima 1998, Peckarsky et al. 2008). Stream communities are regarded as particularly open systems where trait-mediated, or non-consumptive effects of predators on prey are particularly important (Peckarsky et al. 2008). Therefore, the changes in prey and algal biomass in this experiment, could have been caused by a number of different predator-related mechanisms, and not just through their direct

consumptive effects. However, regardless of the proximate mechanisms, my results are still broadly consistent with allometric theory, likely because all activities of predators, including their movements and other behaviours that might influence prey behaviour, incur metabolic demands.

The decreased prey biomass in channels with smaller more numerous top predators caused there to be increasingly more predator biomass relative to prey biomass. Traditional Eltonian pyramids depict the number or biomass of organisms/species at different trophic levels in a community, with predators at the apex of the pyramid and prey at the base. The shape of these pyramids can provide information on the structure and potentially stability of particular community structures (Raffaelli 2002, Rip and McCann 2011, Trebilco et al. 2013). Although, the predator-prey ratio used in this experiment is only a coarse equivalent of a biomass pyramid, an increasing ratio of predators to prey is an indication of increasingly top heavy biomass pyramids. Unless predators are subsidised by an external resource subsidy which is disconnected from production at the base of the food web, then top heavy biomass pyramids are indicative of inherently unstable food-web structures (Rip and McCann 2011, Trebilco et al. 2013). Therefore, it is likely that by decreasing predator size, but not changing the biomass of top predators, inherently unstable communities were created. Consequently, if the experiment had been run over a longer time period it is unlikely that the prey biomass would have been insufficient to support the abundant small predators, potentially resulting in top predator population collapse.

It is also likely that particularly strong intraspecific competitive interactions, when predators were more abundant, also caused more unstable predator communities in this experiment. Increased competitive, interactions such as mutual interference, can be stabilising if they reduce strong effects of predation on lower trophic levels (Arditi et al. 2004, DeLong and

Vasseur 2013). However, strong competitive interactions, which were likely present in this experiment, can also lead to inherently unstable predator populations (DeLong and Vasseur 2013). There was a non-linear relationship between predator abundance, prey and algal biomass in the channels when the highest predator density and biomass treatment were included in the analyses, indicating a weakening top-down effect of predators at high top predator abundances. This could have occurred because either the prey in the channels were already depressed to a level where predators were substantially limited by prey availability, or alternatively, substantial predator interference at high predator densities outweighed direct predation effects. Moreover, it is likely that limited prey availability in the high density, small predator, treatments could have caused a negative feedback cycle, where small predators depress resources faster than large less abundant predators and thus enhance already potentially strong competitive interactions.

Further evidence of mutual interference between individuals could be seen by inspecting fin damage in euthanised fish at the end of the experiment (Figure S 2). Brown trout are an aggressive species (Deverill et al. 1999) and therefore, in channels with a high abundance of individuals strong mutual interference would be expected. The experiment was ended when it significant signs of fin damage were detected. Therefore, the effects of predators on prey seen in this experiment should reflect the strongest interactions before the predator populations were likely to crash. The high levels of mutual interference observed in these experiments further indicate that the communities with many small predators would likely be unstable, and therefore unsustainable in the long term.

In this experiment, different predator size classes had significantly different impacts on lower trophic levels, which would not be predicted if top predator biomass was lumped together in one food web node. Therefore, in a food-web context the results of this experiment provide

support for the use of individual or size-class-based food webs (e.g. Woodward et al. 2010, Gilljam et al. 2011), particularly in size-structured systems, rather than the traditional species node food webs. Additionally, this experiment has highlighted that more small predators compared to fewer larger predators of equivalent biomass have stronger top-down effects on lower trophic levels and therefore require more prey biomass production for long-term stability. Consequently, a fixed quantity of prey resource in an ecosystem should be able to support more predator biomass if they are large bodied. This emphasises the importance of the conservation of large top predators in food webs, because changes to communities which shift the predator body size distribution towards smaller individuals have the potential to increase top-down effects and de-stabilise food webs in the short term, reducing the predator biomass able to be supported in the long term.

Supplementary material

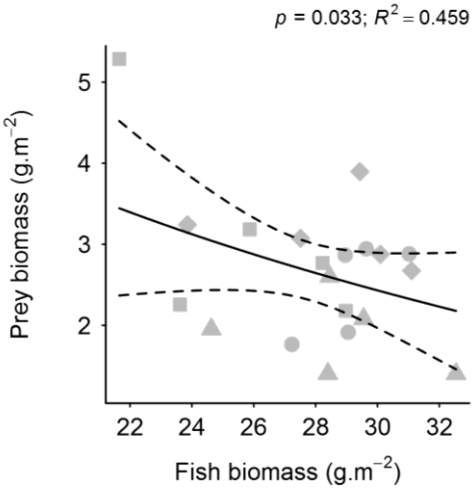


Figure S 1. Relationship between fish biomass and prey biomass. Biomass was measured in grams of dry weight per m^2. The different symbols represent the four different blocks. Significant regression lines and 95% confidence intervals fit from the fish biomass main effect accounting for any block effect are plotted. The p-value associated with the number of fish main effect and the R^2 for the full model including the block effect are displayed. The number of fish axis was log transformed for the analysis and the regression line and axis has been back-transformed for plotting.

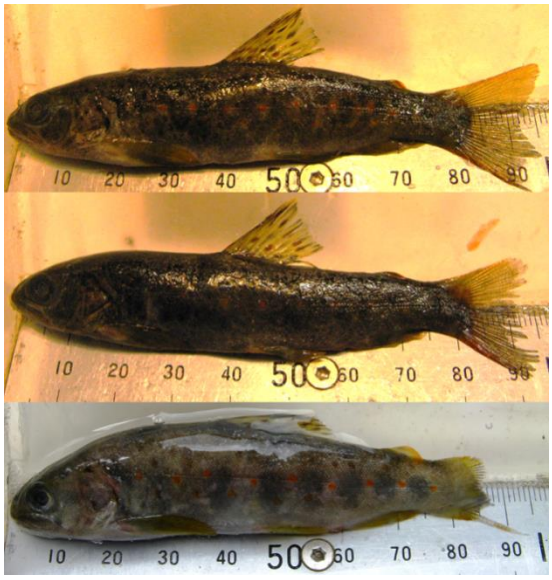


Figure S 2. Photographs of euthanised fish after the experiment. All three fish are from the smallest size class treatment (13 per channel) and the fin damage, especially to the caudal fin, are indicative of significant mutual interference between individuals within channels.

Table S 1. Analysis of variance results showing the number of fish and block effects on the biomass of fish in all the treatments (a) and in the treatments with 2, 4, and 7 fish where biomass was balanced (b).

	df	SS	F	P
a) All treatments				
Number of fish	1	61.69	19.07	< 0.001
Block	3	37.51	3.86	0.031
Residual	15	48.53		
Model R^2= 0.67				
b) Fish biomass balanced treatments				
Number of fish	1	5.22	2.31	0.172
Block	3	15.62	2.31	0.163
Residual	7	15.80		
Model R^2= 0.57				

Table S 2. Analysis of variance results showing the number of fish and block effects on prey biomass (a), predatory invertebrate biomass (b), algal biomass (c), and the predator: prey biomass ratio (d), in the three treatments (2, 4, 7 fish per channel) where fish biomass was balanced.

	df	SS	F	P
a) Prey Biomass				
Number of fish	1	2.77	6.89	0.034
Block	3	5.94	4.92	0.038
Residual	7	2.82		
Model R^2 = 0.76				
b) Predatory invertebrate biomass				
Number of fish	1	0.005	0.55	0.483
Block	3	0.058	1.92	0.215
Residual	7	0.070		
Model R^2 = 0.47				
c) Algal biomass				
Log_{10} Number of fish	1	1.28	5.49	0.051
Block	3	0.13	0.18	0.904
Residual	7	1.63		
Model R^2 = 0.46				
d) Predator:prey biomass ratio				
Number of fish	1	0.061	14.55	0.007
Block	3	0.088	6.97	0.016
Residual	7	0.029		
Model R^2 = 0.84				

Table S 3. Analysis of variance results showing the number of fish and block effects on prey biomass (a), and algal biomass (b) in all the treatments (1, 2, 4, 7, 13 fish per channel).

	df	SS	F	P
a) Prey biomass				
Log_{10} Number of fish	1	6.13	6.40	0.023
Block	3	11.61	4.04	0.027
Residual	15	14.37		
Model $R^2 = 0.55$				
b) Algal biomass				
Log_{10} Number of fish	1	4.24	17.81	< 0.001
Block	3	1.21	1.69	0.212
Residual	15	3.57		
Model $R^2 = 0.60$				

Chapter Six

Discussion

The growing body of research showing consistent and predictable patterns related to body size in ecological networks, particularly food webs, suggests that body size might be a particularly informative variable for understanding many of the complexities associated with natural communities (Woodward et al. 2005). Many of these patterns are underpinned by the allometric scaling between body size and metabolism, thought to be integral to the relationships seen with body size in ecological communities (Brown et al. 2004). Although the exact exponents of different allometric scaling relationships with body size and even the fundamentals of metabolic theory are debated (Glazier 2015), such relationships provide testable baseline hypotheses, with underlying mechanisms, for empirical ecologists to consider. In this thesis I focused on two key relationships with body size in aquatic communities, firstly, body mass (size)-abundance (M-N) scaling, and secondly, the relationship between body size and top down predator-prey interactions. My results indicate that body size is a useful variable; it can be used to represent changes in community structure, and is related to interaction strengths and the degree of top down control in food webs. However, I have also shown significant deviations from theoretical expectations based on allometric and metabolic theory caused by both changing abiotic conditions and traits over and above body size. In this discussion chapter I summarise key results from each of my chapters using the framework provided by body size and metabolic theory, to illustrate how each contributes to existing theory, and to highlight how my research could be used to improve the current understanding of predator-prey interactions, mechanisms controlling community structure, and the use of body size based theory in ecological management.

Environmental gradients and body size

Abiotic conditions place important constraints on biotic communities (Power et al. 1988, Wellborn et al. 1996). These constraints are best illustrated by community changes across environmental gradients that reveal important mechanisms driving changes in community assemblages (e.g. Wellborn et al. 1996). Body mass-abundance relationships summarise the complexities of community structure, and theory predicts slopes of M-N relationships should be approximately - 0.75 within a trophic level, or - 1 across multiple trophic levels, largely based on biotic mechanisms related to predator-prey interactions and energetic transfer efficiencies (Jennings 2005, White et al. 2007, Trebilco et al. 2013). However, physical constraints differentially affecting particular size classes of organisms have potential to alter slopes of M-N relationships, despite these hypothesised biotic regulating mechanisms. In Chapter Two I investigated how M-N slope changed across a habitat-size gradient. Habitat size limited the size of top predators, but not the size of smallest organisms, thus changing the M-N slope and mass range attributes of the M-N relationship (Chapter Two). Although these results do not necessarily directly support theory proposing consistent slopes of the scaling relationship between M and N across communities, they highlight how M-N relationships, and changes in body size patterns across communities generally, are particularly useful tools for understanding influences on community structure.

In addition to providing information on specific changes in community structure, deviations from theoretical predictions in M-N relationships highlight situations in which traits and processes, over and above those related to body size, might be particularly important. Moreover, because M-N data provide rich information on community structure, and are relatively easy to collect, they could be incorporated more in biomonitoring. Body mass-abundance relationships have been used in the monitoring and impact assessment of marine

fisheries (Rice and Gislason 1996, Shin et al. 2005), but seldom used in monitoring other systems. M-N relationships should also be especially useful in summarising change in communities that are already highly-size structured. Therefore, ecosystems which are often highly size structured, like streams and lakes, are likely to be suitable for using M-N relationships as a biomonitoring tool.

Furthermore, M-N relationships may also help fill important gaps in the often disconnected branches of theoretical and applied ecology. Recently, there has been a call for more information on the structure of biological networks to be used in biomonitoring and management, because ecological function is inherently dependent on the interactions summarised in networks (Tylianakis et al. 2010, Thompson et al. 2012, Gray et al. 2014). Body mass-abundance relationships, although not directly representing network connections, provide a tractable, and much more complete summary of community structure than species abundance or richness data alone and are taxon-independent allowing potential comparison across systems with different species. Linking ecological theory and ecological management through use of M-N relationships not only has the potential to improve biomonitoring and assessment, but should also contribute to continued development of body-size related theory; there would be larger collections of data allowing generalities and exceptions to be more readily identified.

Traits and interaction strengths

In addition to body size, other traits, such as morphological defences, are likely to change across environmental gradients. For example, across flooding disturbance gradients the composition of invertebrate prey generally transitions from a highly mobile, but vulnerable to predation, mayfly dominated fauna, to less mobile but defended from predation consumers dominated by cased consumers like caddisflies (Wootton et al. 1996, Jellyman 2011). Such

changes in traits have the potential to alter important biotic processes in food webs that would not be predicted by the current body size-related theories which are largely built on metabolic processes. For example, in Chapter Three I showed that prey defences significantly reduce predator-prey interaction strengths across a gradient of body size defined by predator-prey mass ratios (PPMRs), and in Chapter Four I showed that prey abundance also significantly altered the relationship between PPMR and interaction strength. In both these sets of findings, body size still played an important role in determining predator-prey interaction strengths. However, estimating the many interaction strengths in food webs could be improved by incorporating these other traits into current theory and modelling.

A main benefit of using body size to estimate food web interaction strengths is that it is easy to measure and generally applicable across taxonomic boundaries. Therefore, the addition of extra traits to current practice, should aim to maintain both generality and ease of measurement. For example, Boukal (2014) recently proposed a lock-and-key hypothesis for summarising how traits of predators and prey were important for determining whether potential food web links were realised and how strong those interactions were. The lock-and-key analogy is based on predators having a set of foraging traits which allow them to successfully unlock (find and capture) their prey. It is likely that the matching of a few general foraging traits of predators, such as foraging mode, detection mode and feeding mode, with a few general prey vulnerability traits, such as defences and behaviour, over and above body size could improve the realism of interaction strength estimates based solely on body size (Rossberg et al. 2010, Klecka and Boukal 2013, Boukal 2014).

Although predicting realised links in food webs (connectance) and interaction strengths are commonly separated in the literature, they are essentially two different stages of the same process; for there to be an interaction strength there first has to be an interaction. Therefore,

traits, over and above body size, that affect interaction strengths may be able to be identified by examining patterns in existing connectance-based food webs. These traits could then be used to develop testable hypothesis about which traits are important for determining interaction strengths.

Body size and community dynamics

In addition to showing that predictions based on body size-related theory are dependent on both environmental conditions and additional traits of prey, Chapter Five highlighted the importance of considering body size in top-down trophic interactions structuring food webs. In my experiment, prey biomass was depleted significantly more in the treatments with many small predators compared to few larger predators, and evidence of significant mutual interference indicated that treatments with many small predators would be unstable and vulnerable to collapse in the long term. Therefore, my Chapter Five results show how important it is to consider how top-predator biomass is divided amongst predators of differing body size. Importantly, a given biomass consisting of many small predators will have a higher population energetic (metabolic) demand compared to few larger predators, so lumping top predator biomass can hide important differences in feeding rates of different sized predators.

As well as connecting community dynamics with body size, my Chapter Five experiment was a test of the mechanisms behind patterns observed across a habitat size gradient in hydrologically stable streams in the Cass Region, New Zealand (McIntosh et al. Unpublished manuscript). These stable streams have increasingly top-heavy biomass pyramids (higher predator relative to prey biomass) as habitat size increases, associated with increasing predator sizes, suggesting capacity to support top-predator biomass increases with habitat size. Patterns related to body size identified by sampling across different gradients (e.g.

Chapter Two) reflect the end-result of community assembly and describe communities persisting in the particular habitat sampled. Manipulative experiments are useful for determining the mechanisms that driving such community changes. For example, my Chapter Five experimental results provide mechanistic insights which helped explain survey patterns and supported the idea that more top-heavy food webs can be supported in larger streams because predators are fewer and larger.

Although communities most often observed in nature have evidently persisted, certain distributions of body sizes might be less resistant and/or resilient to future perturbations. For example, shallow slopes of M-N relationships may be less resistant and resilient, because shallow slopes indicate more predators relative to prey. However, although changes in body size distributions reflected in M-N relationships may indicate more or less stable community structures, experimental evidence connecting changes in body size distributions to stability in food webs has often been lacking. If further experiments can mechanistically link changes in body size distributions, for example associated with habitat size, community stability and potentially function, then M-N relationships will become a particularly powerful tool for assessing community states and their likely consequences.

Predator size, habitat size, defended prey and changes in community stability – an example

Throughout this thesis I have highlighted how body size can be used to summarise aspects of both community structure and the strength of interactions in food webs, both of which are important drivers of food web stability (McCann 2000, Dunne et al. 2002, Neutel et al. 2002). I have also demonstrated that physical conditions drive changes in body size distributions, reflecting changes in community structure, and that other traits, over and above body size, also influence the strength of interactions in freshwater food webs. In the following section I illustrate how this information could be used to predict changes to community structure and

stability when, for example, converting a stream from a large disturbed stream to a smaller stable stream. This is the most extreme example possible, but it serves to illustrate the application of my findings.

Since habitat size affects body size distributions, primarily through constraining top predator size (Chapter Two) top predator size is likely to decrease with reduced habitat size. Based on results from Chapter Five, this decrease in top predator size, in the short term, should create an unstable community, because more small predators in a population would have stronger top-down interactions, and would ultimately require more prey resource than the same biomass of larger predators to support their population. Consequently, in a stable stream, a long-term decrease in habitat size should support fewer predators for a unit of prey biomass.

Disturbance also influences prey traits. Prey in disturbed streams tend to be mobile and lack morphological defences, while prey in stable streams tend to be morphologically defended and sedentary (Wootton et al. 1996, Jellyman 2011). Therefore, extrapolating from Chapter Three, under more stable flows, I would expect top predators to have significantly weaker interaction strengths because their prey are less palatable and therefore effectively less available as a food resource for predators. This additional information on prey defences means that communities in small stable streams should be even less stable than predicted by mechanisms based on body size alone. This higher proportion of defended prey means that there would be less available prey resource for top fish predators, which would likely interact with the increased energetic demands of smaller predators to create an even more unstable community. These simple extrapolations have potentially important implications for the management of waterways and changing flow regimes. They also highlight how both body size, other traits of prey, and an understanding of how an environmental gradients interact

with these, can be used to make mechanistic predictions about resulting food web structure and stability. A future challenge is to conduct more experiments to test these predictions.

Conclusions

Overall my results demonstrate that body size is a particularly useful proxy variable to measure for summarising community structure and interaction strengths. However, I have also shown that the relationships between body size and interaction strengths in food webs are likely to be influence by additional organism traits and processes over and above those predicted by body size and metabolic processes. Specifically, prey defences and prey abundance can alter the scaling relationship between interaction strengths and PPMRs. An important area of future research is to incorporate these additional traits into interaction strength metrics to improve modelling of interaction strengths across different communities. I have also highlighted that changes in body size distributions can underpin important changes in community structure and therefore, could become a potentially informative biomonitoring tool. Moreover, if future research can empirically link the mechanisms behind changes in body size distributions to food web stability and function, then measures of body size distributions across communities, such as M-N relationships, will become a potentially very powerful tool in both basic and applied ecology.

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